BULLETIN
of CARNEGIE MUSEUM OF NATURAL HISTORY

RELATIONSHIPS OF SOME INSECTIVORES AND RODENTS FROM THE MIOCENE OF NORTH AMERICA AND EUROPE

BURKART ENGESSER
Resident Museum Specialist, Section of Vertebrate Fossils
(permanent address: Naturhistorisches Museum,
Basel, Switzerland)

NUMBER 14 PITTSBURGH, 1979

BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY
Number 14, pages 1–68, figures 1–12, table 1, plates 1–20

Issued 14 May 1979

Price: $5.00 a copy

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CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

CONTENTS

Abstract 5
Zusammenfassung 5
Résumé 5
Introduction 6
Acknowledgments 7
Relationships of Insectivores 7
  Lanthanotherium 7
  Plesiosorex/Meterix 9
  Subfamily Heterosoricinae Viret and Zapfe 1951 12
  Limnoecus 19
Relationships of Rodents 20
  "*Sciuropterus*" 20
    Petauristodon, new genus 23
  Family Eomyidae Depéret and Douxami, 1902 23
    Pseudotheridomys 24
    Leptodontomys 25
    Eomyops, new genus 27
  Cotimus, *Leidymys*, *Eumyarion*, and *Eucricetodon* 28
  Democricetodon and *Copemys* 31
  Plesiosminthus 35
Discussion 39
  Migration 39
  Parallel Evolution 41
Conclusion 42
Literature Cited 42
Plates 46

ABSTRACT

Ten genera of Miocene small mammals from Europe are compared with similar forms, regarded as congeneric by many authors, from North America. These are *Lanthanotherium*, *Plesiosorex*, "*Trimylus*"/*Heterosorex*, *Limnoecus*, "*Sciuropterus*," *Pseudotheridomys*, *Leptodontomys*, "*Cotimus*," *Democricetodon*/*Copemys*, and *Plesiosminthus*. On the basis of morphological differences, the European eomyids hitherto assigned to *Leptodontomys* are here separated from this genus and united in the new genus *Eomyops*. For the North American rodents so far described as "*Sciuropterus*" the new genus *Petauristodon* is introduced. The newly discovered upper dentition of "*Cotimus*" *alicae* shows that Schaub's "*Cricetodon heveticus*" and related forms from Europe, assigned to the American genus "*Cotimus*" (=*Leidymys*) by several authors, have nothing to do with this genus. The European forms are merged within another genus for which the name *Eumyarion* Thaler, 1966, should be used. The European heterosoricine genera *Quercysorex*, *Heterosorex*, and *Dinosorex* are differentiated morphologically from the American genera *Domnina* and *Pseudotrimylus*. Some small soricids from Europe assigned by many authors to the American subfamily Limnoecinae are compared with representatives of the genus *Limnoecus*. These comparisons led to the conclusion that at present there is no reason to include any European form in this American subfamily.

The discussion attempts to show that in addition to migration other possibilities, such as parallelism and persistence of primitive characters over long periods, must be considered to explain the close similarities of some forms from both continents.

ZUSAMMENFASSUNG

Zehn miozäne Kleinsäuger-Formen Europas werden mit ähnlichen Formen aus Nordamerika verglichen, mit welchen zusammen sie bisher in die gleiche Gattung gestellt wurden: *Lanthanotherium*, *Plesiosorex*, "*Trimylus*"/*Heterosorex*, *Limnoecus*, "*Sciuropterus*," *Pseudotheriodomys*, *Leptodontomys*, "*Cotimus*," *Democricetodon*/*Copemys*, *Plesiosminthus*. Aufgrund morphologischer Unterschiede werden die bisher *Leptodontomys* zugeordneten Eomyiden Europas von diesem Genus abgetrennt und im neu geschaffenen Genus *Eomyops* vereinigt. Für die bisher als "*Sciuropterus*" beschriebenen Formen Nordamerikas wird das neue Genus *Petauristodon* aufgestellt. Funde der bisher unbekannten Maxillarbezahnung von "*Cotimus*" *alicae* haben gezeigt, dass Schaubs "*Cricetodon helveticus*" und verwandte Formen Europas, welche von manchen Autoren dem amerikanischen Genus "*Cotimus*" (=*Leidymys*) zugeordnet wurden, nichts mit diesem Genus zu tun haben. Sie sind im Genus *Eumyarion* Thaler 1966 zu vereinigen. Die europäischen Heterosoricinae-Genera *Quercysorex*, *Heterosorex* und *Dinosorex* werden gegen die amerikanischen Genera *Domnina* und *Pseudotrimylus* morphologisch abgegrenzt. Die von manchen Autoren der amerikanischen Unterfamilie Limnoecinae zugeordneten kleinen Soriciden Europas werden mit Vertretern der Gattung *Limnoecus* verglichen. Dabei zeigt sich, dass gegenwärtig keine Veranlassung besteht, irgendwelche europäischen Formen in diese amerikanische Unterfamilie zue stellen.

Im allgemeinen Teil wird zu zeigen versucht, dass als Erklärung für das Zustandekommen der erstaunlichen Aehnlichkeiten von Formen beider Kontinente, neben der Migration auch noch mit andern Möglichkeiten wie Parallelentwicklungen und Beibehaltung primitiver Merkmale über lange Zeitraume zu rechnen ist.

RÉSUMÉ

Dix micromammifères miocènes d'Europe sont comparés à des formes semblables de l'Amérique du Nord qui figuraient jusqu'ici dans le même genre: *Lanthanotherium*, *Plesiosorex*, "*Trimylus*"/*Heterosorex*, *Limnoecus*, "*Sciuropterus*," *Pseudotheridomys*, *Leptodontomys*, "*Cotimus*," *Democricetodon*/*Copemys*, *Plesiosminthus*. En raison de différences morphologiques, les éomidés d'Europe sont séparés du genre *Leptodontomys* auquel ils avaient été attribués et sont réunis dans le genre *Eomyops* nouvellement créé. Pur les formes américaines décrites auparavant, comme "*Sciuropterus*," un nouveau genre, *Petauristodon*, est établi. La découverte de dents de maxillaires de "*Cotimus*" *alicae* inconnues jusqu'à présent a montré que le "*Cricetodon helveticus*" de Schaub et d'autres formes apparentées d'Europe, attribuées par plusieurs auteurs au genre américain "*Cotimus*" (=*Leidymys*), n'avaient rien à voir avec ce genre. Ces formes doivent être réunies dans le genre *Eumyarion* Thaler 1966. Les genres européens d'hétérosoricinés, *Quercysorex*, *Heterosorex* et *Dinosorex* sont distingués morphologiquement des genres américains *Domnina* et *Pseudotrimylus*. Les petits soricidés d'Europe, attribués par plusieurs auteurs à la sous-famille des limnoecinés sont comparés à des représentants du genre *Limnoecus*. Ces comparaisons ont démontré qu'il n'y a actuellement pas de raison de placer l'une ou l'autre des formes européennes dans cette sous-famille.

Dans la partie générale, on tente de démontrer que l'étonnante ressemblance des formes des deux continents peut être expliquée outre la migration, par d'autres possibilités telles que l'évolution parallèle et la persistance des caractères primitifs pendant de très longues périodes.

INTRODUCTION

This paper is an experiment. A great number of questions are asked, but to only a few can an answer be given.

During the last few years several species of European mammals have frequently been united in the same genus as North American species, almost always on the basis of similarities in tooth morphology. The presence of such similar forms on both continents was usually explained by intercontinental faunal exchange or, as most authors state, by "migration."

In this study I tried to approach the problems from a different point of view from that of most authors having worked in this field. In many cases I intentionally took the part of the *advocatus diaboli*. My main object with this was to re-open several issues so that some problems will be discussed again. Many problems of relationships between Tertiary mammalian faunas from North America and Europe are regarded as solved and are not discussed anymore. In my opinion it is premature to give a solution to such complicated problems on the basis of the scanty available comparative material. For the solution we need more complete and abundant specimens. In addition, in the course of this study I began to doubt whether tooth morphology alone can be trusted for the clarification of phylogenetic relations, especially for such higher systematic categories as genus, subfamily, or family.

In this paper I try to show that in addition to faunal exchange other possibilities must still be considered, including parallelism and the persistence of primitive forms on both continents over long periods. In most cases no material was available other than that from which my colleagues had drawn their conclusions, so I tried to apply other morphologic criteria. I also examined earlier faunas of both continents to determine whether there are forms from which the latter forms, showing similarities to those of the other continent, could be derived (without supposing a lateral communication). Thus, starting with upper Miocene genera being reported to occur on both continents, I also studied small mammals from the Lower Miocene, the Oligocene, and, in some cases, the Eocene.

For this study I selected ten genera that appeared to me to be especially rewarding and with which I had the possibility of comparing American and European original specimens. I endeavored to compare as many different groups as possible, because conclusions can follow from a broad spectrum of forms that cannot be drawn from one group. Because of the abundance of forms, and because the magnitude of the subject required me to follow the different groups over long periods—sometimes through the whole Tertiary—I confined myself to the rodents and insectivores.

Assuming that most readers will not read through the whole paper, but rather will confine themselves to chapters interesting to them, the different chapters are self-contained. This involved, of course, some repetition in the different chapters.

Because the time correlations of North American and European mammal faunas still are very much a matter of discussion, I abstained from giving a correlation table and correlated only on the level of epochs. The term "Miocene" is used in the modern sense, that is, the period between ca. 23 and 5 million years ago; likewise the Pliocene, which covers the period between 5 and 1.8 million years ago. For North American stratigraphy, I used the current land mammal ages such as Arikareean, Hemingfordian, and so forth, but for the European Neogene I largely refrained from using terms like Helvetian, Tortonian, Sarmatian, and others. These are mostly defined on the basis of marine formations and therefore in continental stratigraphy they can mean very different things, according to the country and school of the different authors. So for the European Neogene I used the mammal units NMU 1–16 (NMU = Neogene Mammal Unit), introduced and worked out by Mein (1976). For colleagues not acquainted with this new mammal zonation, I sometimes added the misleading stage names in quotation marks.

Abbreviations of the institutions owning the specimens described and figured in this paper are as follows: AMNH, American Museum of Natural History, New York; BSPM, Bayerische Staatssammlung für Paläontologie und historische Geologie, München; CM, Carnegie Museum of Natural History, Pittsburgh; FSL, Faculté des Sciences de Lyon; KU, University of Kansas Museum of Natural History, Lawrence; MO, Museum Olten (Solothurn, Switzerland); MHNP, Muséum national d'Histoire naturelle, Paris; NHW, Naturhistorisches Museum Wien; NMBS, Naturhistorisches Museum Basel; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; SDSM, South Dakota School of Mines, Museum of Geology, Rapid City; UCMP, University of California Museum of Paleontology, Berkeley; UNSM, University of Nebraska State Museum, Lincoln; UO, University of Oregon, Museum of Natural History, Eugene.

ACKNOWLEDGMENTS

Without the generous help of the Carnegie Museum of Natural History, which offered me a nine month stay as a Resident Museum Specialist, I would not have been able to accomplish this study. Among the staff of this museum I am especially indebted to Dr. Mary Dawson, Dr. M. G. Netting, Dr. J. Swauger, and Mr. W. Woodside. In addition, Dr. Dawson's discussions and criticism have been most helpful in the realization of this work; her help was very much appreciated in correcting the English text. I also wish to thank Dr. L. Krishtalka and Dr. J. H. Hutchison for going over parts of the manuscript. I am also very grateful to Dr. C. C. Black for having the paper published here.

Further, I am indebted to the *Stipendienkommission des Kantons Basel-Stadt* for having provided an additional grant for my stay in the United States and to the Janggen-Pöhn-Foundation (St. Gallen) which enabled me to study European comparative materials in the collections of Lyon and Munich after my return to Europe.

Dr. Johannes Hurzeler followed this study from its beginning with great interest and was always at hand with valuable information and suggestions. I also wish to thank Dr. F. Wiedenmayer and Mr. J. B. Saunders for having helped me with the English translation and Miss H. Pouget and Miss E. Hill for having typed the manuscript. I am grateful to my wife Wies for her help and her patience during the time of this work and especially for having made excellent casts of specimens during our stay in America.

To the following I am indebted for the loan of comparative materials, providing literature and casts, for discussions, information, and criticism, as well as for other kinds of help: Prof. Dr. R. Dehm, Munich; Dr. R. J. Emry, Washington, D.C.; Dr. V. Fahlbusch, Munich; Dr. O. Fejfar, Prague; Dr. E. Heizmann, Stuttgart; Dr. M. Hugueney, Lyon; Dr. D. E. Savage, Dr. J. H. Hutchison, and B. Waters, Berkeley; J. Yarmer, Pittsburgh; Dr. L. Kittleman, Eugene; Dr. E. Lindsay, Tucson; Dr. L. D. Martin, Lawrence; H. McGinnis, Pittsburgh; Drs. M. C. McKenna, J. H. Wahlert, and M. F. Skinner, New York; P. Mein, Lyon; D. L. Rasmussen, Denver; Dr. C. Ray, Washington, D.C.; Dr. P. Robinson, Boulder; Drs. R. Zangerl, W. D. Turnbull, and W. Segall, Chicago; Prof. Dr. H. Tobien, Mainz; Dr. R. W. Wilson, Lawrence; Prof. Dr. H. Zapfe, Wien.

RELATIONSHIPS OF INSECTIVORES

LANTHANOTHERIUM

(Fam. Erinaceidae, Bonaparte, 1838, Subfamily Echinosoricinae Cabrera, 1925)

History of Investigations

The genus *Lanthanotherium* was introduced in 1888 by Filhol for Lartet's *Erinaceus sansaniensis* from Sansan. Outside of *L. sansaniense* four more species have now been described from Europe—*L. robustum* Viret, 1940, from La Grive; *L. longirostre* Thenius, 1949, from Leoben; *L. sanmigueli* Villalta and Crusafont, 1944, from Viladecaballs; and *L. piveteaui* Crusafont, Villalta, and Truyols, 1955, from Can Cerda. A second species from Sansan, described in 1972 by Baudelot as *L. tobieni*, is here considered as a synonym of *L. sansaniense*.[1] Butler (1969) reported *Lanthanotherium* from the Miocene of Africa (Songhor, eastern Africa). I know of no fossils of *Lanthanotherium* from Asia, where all Recent representatives of the Echinosoricinae live. Webb's reference (1961:1085) to a passage in Viret (1940:53) in which a questionable *Lanthanotherium* specimen from China is said to be mentioned, apparently is due to a mistake, because in this passage Viret discusses only the Recent *Neotetracus sinensis* Trouessart, 1909, and the Oligocene *Tetracus* from Ronzon (France). Since 1961 several fossil insectivores from North America were incorporated into the genus *Lanthanotherium*. Webb (1961) assigned a jaw fragment with three molars from the Bopesta Formation (Barstovian) of California to this genus. Subsequently, James (1963) described two new species of *Lanthanotherium*—*L. sawini* and *L. dehmi*. Since then remains of these animals were also reported from the Red Basin in Oregon (Shotwell, 1968) and from the Barstow Formation in California (Lindsay, 1972).

Among the numerous currently described species of *Lanthanotherium* the dentition is known to some extent from only three—*L. sawini*, of which even a well preserved skull fragment is known; *L. sansaniense*; and *L. longirostre*. All the other forms are hitherto documented only by fragments of mandibles. Therefore, in *Lanthanotherium*, as in many genera treated in this paper, all comparisons are limited to the dentition.

As in most insectivore groups, in the Echinosoricinae the molars behave very conservatively during evolution, whereas the anterior part of the dentition undergoes various differentiations. This becomes obvious on comparing the dentitions of

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[1] Baudelot (1972) introduced the species *L. tobieni* chiefly on the basis of a fourth premolar in two lower jaw fragments (*L. sansaniense* usually has three lower premolars). It is generally known that the number of premolars in Echinosoricinae varies considerably within a population, often even in the two halves of one jaw. Van Valen (1967:272), for example, described three skulls of the Recent species *Hylomys suillus*—one specimen had three P on both sides; another, four P on both sides; and a third specimen, three P on the right upper jaw and four on the left. According to Van Valen, the same variability can be observed in the Recent *Neotetracus sinensis* and I found the same variability also in lower jaws of Echinosoricinae in our collection.

Neurogymnurus and *Lanthanotherium*, for example. Therefore, at the generic level more systematic value must be attached to differences in molars than to those of the anterior dentition. The same observation can be made comparing the European species of *Lanthanotherium*—the anterior dentition shows very important differences, the molar dentition hardly any.

Comparisons of American and European Forms

Because, as James (1963) pointed out, the best documented American species, *L. sawini*, shows a highly specialized anterior dentition, the following comparisons are restricted to molar morphology. Thus, I tried to distinguish the features in common to forms on one continent and compared them with the characteristics of the forms on the other continent. Determination of the typical features of the American species of *Lanthanotherium* was greatly aided by examination of excellent material from an unpublished fauna (I was requested not to mention this material, specifically, but as a check on my conclusions it was very helpful). Viret (1940) and Butler (1948) showed that the third upper molar in the Erinaceidae is taxonomically significant. I found $M^3/M_3$to differ between the species on the two continents—these differences I interpret as general ones.

M^3 of American *Lanthanotherium* is more reduced compared with those of European species. The parastyle and anterior cingulum are less developed and, sometimes, lacking, a feature never observed in European forms (see Plate 1). The anterior crest of the protocone extends directly to the paracone, rather than to the anterolabial corner of the tooth (the parastyle) as in European species of *Lanthanotherium*. On M^3 of the American species the cusps are less distinct and fused to a ring-shaped wall that is open only on the lingual side. The cusp on the posterior corner of the tooth[2], especially well developed in *L. sansaniense*, (Plate 1a) is less well differentiated in American forms. The posterior crest of the protocone in European species extends to the metacone, leaving a distinct lingual shelf. On M^3 of American specimens this posterior protocone crest ends shortly beyond the protocone or extends to the cusp on the posterior corner of the tooth. The shelf between the posterior branch of the protocone and the lingual tooth margin is lacking or only weakly developed.

On M^2 of American species of *Lanthanotherium* the anterior cingulum is less well developed than that of European forms. The paracone and metacone are connected by a longitudinal crest, which is weakly expressed on corresponding teeth from Europe (Plate 1a–c). In addition, the valley in the posterior half of the tooth between the metacone and hypocone is larger in American forms.

M^1 of American forms is relatively short and its metaconule is crescent-shaped in occlusal view, whereas it is more nearly round in European species. Otherwise M^1 of American and European forms are the most similar of all the upper molars.

Even fewer differences can be observed between the lower molars of American and European species of *Lanthanotherium* (Plate 2). This is not too surprising since the lower molars of different echinosoricines resemble each other very closely (for example, those of *Lanthanotherium*, *Neurogymnurus*, and *Hylomys*).

As already mentioned the species on each continent vary considerably as far as the anterior dentition of the lower and upper jaw is concerned. Therefore the anterior dentition seems to me to be very important for the distinction of different species, but not for the definition of higher taxonomic units. However, the robust anterior dentitions exhibited in *L. sawini* and especially *L. dehmi* (see James, 1963) are not known in European forms.

Finally, all described species of *Lanthanotherium* from North America are distinctly smaller than most European forms of the same age. The only exception among European species is that from Can Llobateres, which, although one of the latest forms, has the smallest dimensions (see Plates 1c and 2d).[3]

Discussion

The comparisons of American and European species of *Lanthanotherium* demonstrate that in addition to the great similarity of the dentitions there are also differences. Even if these differences are not very apparent, their significance for systematics should, in my opinion, not be underestimated.

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[2] Butler (1948) and James (1963) designate this cusp as a hypocone. This designation seems somewhat daring to me, because this cusp is lacking in earlier Echinosoricinae, for example, some Galericini or *Neurogymnurus*, and therefore, in my opinion, has to be regarded as a new acquisition. For that reason it would hardly be homologous with a real hypocone.

[3] Whether the form from Can Llobateres is identifiable as *Lanthanotherium sanmigueli* (Villalta and Crusafont, 1944) cannot be decided on the basis of the descriptions and figures in the original publication. However, on the basis of size the form from Can Llobateres corresponds to *L. sanmigueli* from Viladecaballs, which is of about the same age.

If, in addition, one takes into consideration how little various genera of the Echinosoricinae often differ dentally one can question the incorporation of the *Lanthanotherium*-like forms from North America into the genus *Lanthanotherium*. Comparing, for example, the dentition of American *Lanthanotherium* with those of certain Recent echinosoricines such as *Echinosorex*, *Neotetracus*, and *Hylomys* (see Plates 1d and 2e), one notices that the correspondence with the Recent forms is the same as with *Lanthanotherium* from Europe. With the same justification the American *Lanthanotherium* could therefore be assigned to *Hylomys* or *Neotetracus*. For this reason, it seems appropriate to separate generically the American and European species of *Lanthanotherium*. However, I refrain from this action until better skull remains of the European forms are known. New conclusions about the phylogenetic relations can also be expected following study of the unpublished *Lanthanotherium* material in American collections. Finally, the possibility exists that if more complete remains of *Ocajila* from the Wounded Knee area (Macdonald, 1963) become known, generic identity of the latter genus with the American forms hitherto assigned to *Lanthanotherium* may result, so that all American forms could be united into the genus *Ocajila*.

Even if the dental differences of American and European species of *Lanthanotherium* seem to justify a generic separation, close relationship between the forms from both continents cannot be contested, and with good reason are united with the Recent "moon rats" in the tribe Echinosoricini (Butler, 1948; Van Valen, 1967). How closely these forms are related cannot be judged for the moment, because of the general conservative nature of the dentitions in echinosoricines. A pertinent question here is when the Echinosoricinae (*sensu* Butler, 1948) appeared in the New World. Either this group had already reached America from Europe in the Upper Eocene, or it originated there. An *Ocajila*-like erinaceid is known from the Uintan Tepee Trail Formation of Wyoming (I am indebted to Prof. Robert Wilson for sending me a photocopy of a letter from Dr. Peter Robinson, in which this form is mentioned). This genus, originally described from the Sharps Formation (lower Arikareean), is generally regarded as a member of the Echinosoricinae and is therefore the earliest known representative of this subfamily in the New World. Unfortunately, I have not seen specimens of the Eocene Erinaceid, and only part of the lower dentition of the Wounded Knee species is known (the jaw fragment of Macdonald's figure 4 [1970] is obviously not of *Ocajila* but of a heterocoricine; see also Hutchison, 1972:13). The lower molars of *Ocajila* and *Lanthanotherium* are remarkably alike (see Plate 2c), except that the latter have a somewhat longer trigonid. Based on these, admittedly poor, remains there is no feature in the dentition of *Ocajila* which would exclude this genus from the ancestry of *Lanthanotherium*. In Europe the earliest known echinosoricines are the Middle Oligocene genera *Neurogymnurus* and *Tetracus*, either of which may have given rise to *Lanthanotherium*.

The first appearance of *Lanthanotherium* in Europe is in the Lower Miocene of Vieux Collonges (NMU 4), but in America it is not until the Upper Miocene (Barstovian). On both continents *Lanthanotherium* is recorded until the Upper Miocene (Turolian in Europe, Clarendonian in North America).

If we attribute the dental resemblances between European and North American species assigned to *Lanthanotherium* to intercontinental migration, the Bering Strait is the only possible migration route after the end of the Eocene. There, as with other groups (for example, *Sciuropterus*) treated in this paper, a problem arises—all Recent Echinosoricinae are dwellers of tropical or subtropical forests. From this we can conclude, if conclusions based on analogy with living forms are valid, that the fossil forms ecologically did not behave much differently. For dwellers of tropical forests the far north Bering Strait region should not be underestimated as a climatic barrier (see Simpson, 1947:651: "there is no evidence from the mammals that any truly tropical or subtropical animal ever migrated between Eurasia and North America"). Other ecological barriers likely also existed on this long route. In addition it has to be remembered that no Tertiary Echinosoricinae have yet been found in Asia.

Really we are still groping in the dark with the reconstruction of the history of *Lanthanotherium*. The only statement on which we are on firm ground is that of the morphological differences of the dentition, and from these the conclusion that there should be generic separation for the American and European forms seems to be justified.

PLESIOSOREX/METERIX

(Family Plesiosoricidae Winge, 1917)

The discussion on *Plesiosorex* is confined to points bearing on the relationship between North

American and European forms. A monographic treatment of *Plesiosorex* is in preparation. Also not discussed is the systematic affiliation of this genus, which is still not clear. Wilson (1960) thoroughly compared *Plesiosorex coloradensis* with European species, and therefore I confine myself to some few interesting, comparative points.

Historical Introduction

De Blainville first described in his "Ostéographie" (1838) a representative of this genus under the name *Erinaceus soricinoides*. The type was from the Stampian locality of Chaufours (Limagne, France). Pomel (1854) classified the species from Chaufours with the myogales and introduced the generic name *Plesiosorex*. Dietrich (1929) seems to have been the first author to notice the similarity between the European *Plesiosorex* and the American genus *Meterix* described by Hall (1929). Stromer (1940) incorporated the species *Myogale germanica* (Seemann, 1938) in the genus *Meterix* Hall. In the same year Viret (1940) discussed the phylogenetic relationships of *Plesiosorex* and *Meterix*, and took the view that probably at the end of the "Vindobonian" or the beginning of the "Pontian" representatives of the genus *Plesiosorex* "emigrated" to America. In his monograph on the Quarry A fauna, Wilson (1960) described an insectivore as *Plesiosorex coloradensis*, stating that the Quarry A species showed more similarities with European *Plesiosorex* than with the American *Meterix*.

Comparisons of American and European Forms

Comparisons between European and American plesiosoricids are confined to the dentition, because no other remains of these animals are now known from Europe. Species of *Plesiosorex* from North America and Europe are surprisingly similar and exhibit all the dental features typical of the genus—the paracone and metacone of the upper molars are shifted medially compared with those of other insectivores, and the occurrence of cusps labial to the paracone and metacone. Extensive comparisons of European and North American material failed to reveal fundamental differences in the dentition. Nevertheless, some differences do occur on M^1/M_1, the most diagnostic teeth of *Plesiosorex* apart from I_2.

M^1 of all American *Plesiosorex* known to me shows a relatively strong and well-defined hypocone, whereas this cusp is distinctly lower and less clearly separated from the protocone on M^1 of European species (see Fig. 1c, f, i, and l), such as *P. schaffneri* where the hypocone is essentially a shelf on the posterior side of the protocone (Fig. 1c and Plate 5c).

On M^1 of American species of *Plesiosorex* the cusp labial to the paracone is higher than the latter, whereas in European forms the paracone is always higher (Fig. 1b, e, h, and k). In the North American species the cusp labial to the metacone on M^1 is more developed than in European ones, where it occurs as a crest rather than as a distinct cusp (Fig. 1a, d, g, and j).

Species of *Plesiosorex* from both continents do not differ fundamentally in remaining known parts of the dentition. However, the anterior parts of the dentition are too poorly known for extensive comparisons.

The mandible in American and European Plesiosoricidae are very similar too (see Plate 3).

It is interesting that both the primitive and advanced species of *Plesiosorex* from North America and Europe are very similar to each other. *P. coloradensis*, the earliest and morphologically the most primitive North American form, surprisingly resembles certain primitive species from Europe, for example that from the Rümikon. Both have a relatively short M^1 and a posterior trigon leg (*Trigonumkante*) that runs via the metaconule to the metastyle (Plate 5a and d). More evolved forms from both continents, such as Upper Miocene and Pliocene species of *Meterix* and *Plesiosorex* sp. from Grosslappen have a more elongated M^1, with a posterior trigon leg that ends at the posterior margin of the crown without reaching the metastyle (see Plate 5b and e). Similar observations can be made in the lower dentition—more primitive species on both sides of the Atlantic have an M_1 with a short trigonid compared with the talonid (see Plate 4b and d). In more evolved forms an elongation of the trigonid angle occurs (Plate 4a and c). Also, the number of antemolar teeth apparently becomes more reduced in evolved forms of North America and Europe.

Finally, compared with the more primitive species, the mandible of advanced species from both continents bears a posteriorly shifted mental foramen—the anterior foramen of *P. coloradensis* is below P_2; that of *Meterix* is below P_3 (plate 3a–b). Similarly, among European species of *Plesiosorex* the earlier forms, such as that from St-André (Viret, 1946) and Chaveroche (Plate 3d) bear the anterior foramen below the space between P_1 and

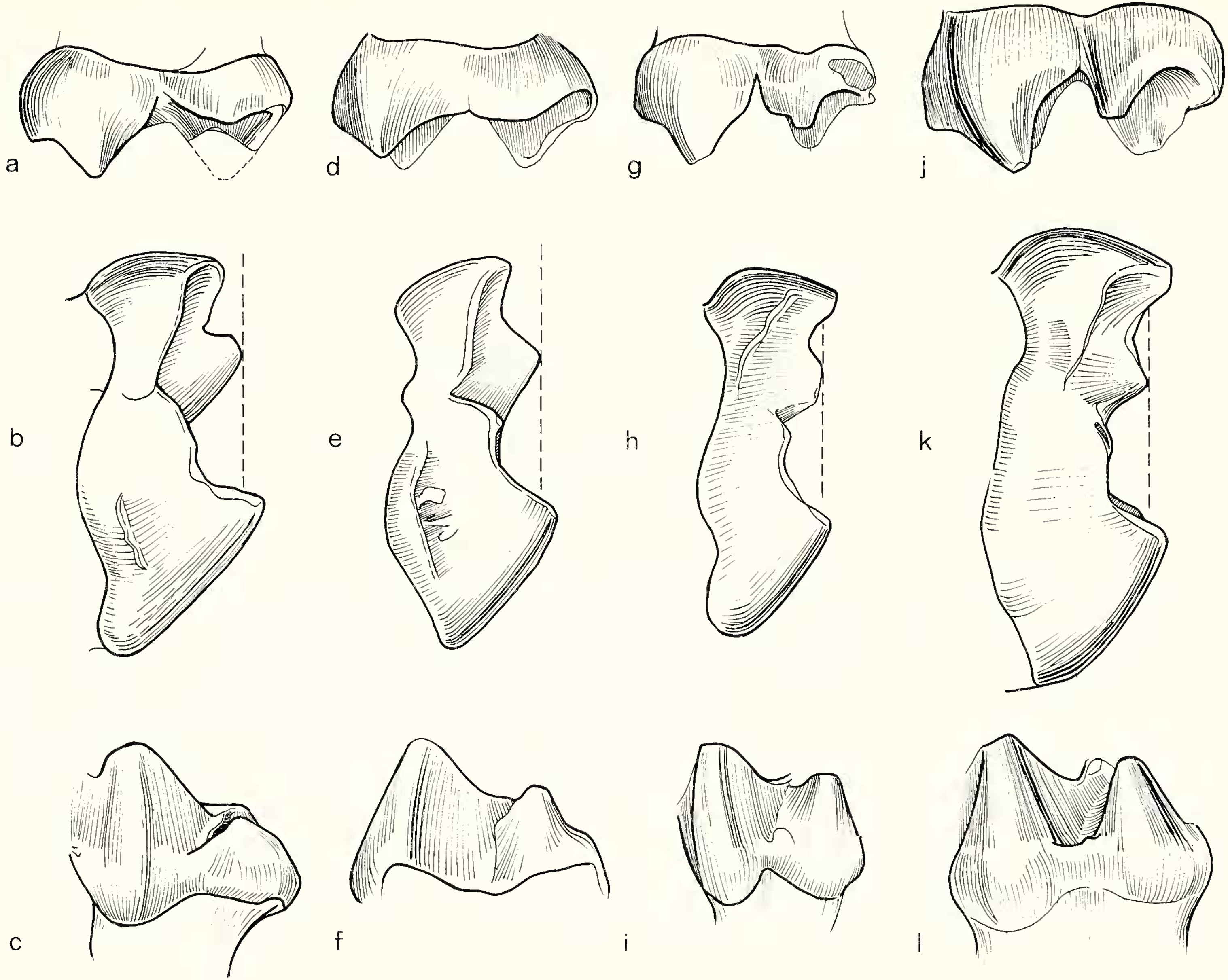

Fig. 1.—Different views of LM^1 of North American and European Plesiosoricidae. Upper row: lingual view; middle row: front view; lower row: labial view. a–c) *Plesiosorex schaffneri* Engesser, a and c: NMBS, Al. 145 (invers), b: NMBS, Al. 538, Anwil (Switzerland), Middle Miocene; d–f) *Plesiosorex* sp., BSPM 1926 I. 81 (invers), Grosslappen (Germany), Middle Miocene; g–i) *Plesiosorex coloradensis* Wilson, KU 9990 (invers), Quarry A, Martin Canyon, Colorado, Hemingfordian; j–l) *Meterix* sp., a and c: OU 22329 (invers), b: OU 22326 (invers), Ove, Quartz Basin, Oregon, Barstovian. All figures 12×.

P_2, but in more advanced forms, such as that from Aumeister, it occurs below the space between P_3 and P_4. Also, the posterior mental foramen of European forms seems to have moved posteriorly during the course of evolution—in the species from St-André and Chaveroche it occurs below P_4 (or below the interspace between P_4 and M_1), whereas, in more evolved forms (for example, from Viehhausen [Seeman, 1938], Rümikon, and Aumeister) it is below the protoconid of M_1. This posterior migration of the posterior foramen in European forms happened apparently between the Upper Oligocene and the Lower Miocene. In America this trend seems to have been terminated in the Lower Miocene, because, like the geologically younger *Meterix*, *P. coloradensis* has this foramen below M_1 (Plate 3a–b).

As is probable for soricids, the movement of the mental foramen in plesiosoricids can be correlated to an enlargement of the large lower incisor (I_2), which unfortunately is known in only a few species.

The intercontinental similarity among primitive and evolved plesiosoricids cannot, in my opinion, be explained only by faunal exchange, because these would have to have involved frequent "intermigrations." An analogous case involves *Democricetodon* and *Copemys*, where the advanced species (on either continent) are more similar to each other than to the primitive ones. It is very difficult to find an explanation for these phenomena. In my opinion it seems worth considering whether evolutionary trends could be involved, which, proceeding from a common origin, can be conserved over long periods.

Of all described species of *Plesiosorex*, *P. coloradensis* from Quarry A is by far the best known. Wilson (1960) concluded that compared with *P. soricinoides* from St-André and *P.* cf. *soricinoides* from Chaveroche, *P. coloradensis* shows more progressive features, but compared with *P. styriacus* (Steiermark) and *P. germanicus* (Viehhausen) was more primitive.[4]

Unpublished *Plesiosorex* material from Europe are similar to *P. coloradensis* and, considering its age, imply the progressive nature of the latter. The strongly reduced labial cingulum of the lower molars is an especially progressive feature in the dentition of *P. coloradensis*. *P. coloradensis* most closely resembles the Rümikon *Plesiosorex* (canton of Zürich, Switzerland, see Plate 5a). On the basis of the cricetids, the Rümikon fauna (NMU 5) has to be regarded as somewhat older than that from Sansan (NMU 6), but according to Wilson's stratigraphic placement of Quarry A, *P. coloradensis* would be distinctly older than the Rümikon species.

How can the great similarities between North American and European *Plesiosorex* be explained? As mentioned above, Viret (1940) suggested "migration" from Europe to North America immediately before the "Pontian." Wilson (1960) also preferred the possibility of a "migration," but he fixed the time for it somewhat earlier—Lower Miocene—because he regarded *P. coloradensis* as a possible ancestor of *Meterix*.[5]

At present, *P. coloradensis* is the oldest known plesiosoricid in North America; no suitable ancestors are known from the Oligocene or Eocene of North America. Nevertheless, such Paleogene forms as *Geolabis* (=*Metacodon*) show similarities with *Plesiosorex*. As stated by Wilson (1960) most of these similarities have to be considered as common primitive features. In Europe *Plesiosorex* is known from earlier levels, that is, from the Stampian. This and the fact the American and European forms are very similar, at least in those parts that we can compare, implies a faunal exchange.

On the other hand, *Plesiosorex* is dentally primitive, having retained these features over very long periods. That the evolved, latest forms on both continents are surprisingly similar implies the possibility of parallelism. Thus, it is possible that *Plesiosorex* reached North America before the time of its earliest known occurrence, and then developed for a long time in parallel to its European relatives.

SUBFAMILY HETEROSORICINAE VIRET AND ZAPFE, 1951

(Family Soricidae Gray, 1821)

History of Investigations

Since my study of the Miocene mammal fauna from Anwil (1972:73) reported on the history of the European Heterosoricinae, this discussion is limited to the opinions of different authors regarding the relationships between North American and European forms. Since Cope's (1873) description of the genus *Domnina*, heterocoricines have been recovered in North America, but, for a long time, were not considered to have a close relationship with European forms. Patterson and McGrew (1937) were the first to point out the similarity of *Domnina* to the European *Heterosorex*, but they did not alter their systematics. Mawby (1960) noted the great resemblance of "*Domnina*" *compressa* (Galbreath, 1953) to *Heterosorex*[6] Gaillard and assigned "*D.*" *compressa* and an undescribed species from Oregon, =*Pseudotrimylus mawbyi* (Repenning) 1967, to *Heterosorex*. Wilson (1960) referred two species from Quarry A to *Heterosorex—H. roperi* and *Heterosorex* sp.—and compared them exhaustively with European species. Wilson claimed that "*Heterosorex*" *roperi* could not have developed independently from European species since the Oligocene. Since 1960, the names *Trimylus* and *Heterosorex* have also been used for American forms (Hutchison, 1966, 1972; Doben-Florin, 1966; Repenning, 1967). In his revision of the family Soricidae, Repenning (1967) was of the opinion that the European and North American Heterosoricinae likely represent two separate evolutionary lines, but he still included species from Europe and North America in the genus *Trimylus*. Gureev (1971) introduced a new genus, *Pseudotrimylus*, for *Heterosorex roperi* from Quarry A. Crochet (1968) had referred three heterosoricines from the European Oligocene to *Domina*—"*Amphisorex*" *primaevus* Filhol, "*Sorex*" *herrlingensis* Palmowski and Wachendorf, and the heterosoricine from Rickenbach (Switzerland). In 1975, I introduced the genus *Quercysorex* for the former two, and placed the latter in the genus *Dinosorex*.

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[4] Thenius (1949) recommended synonymy of *P. germanicus* and *P. styriacus*, in which he was followed by Wilson (1960). Later I (1972:59) advocated for maintenance of both species.

[5] If a close relationship of American and European plesiosoricids will be confirmed in the future, the generic name *Meterix* probably will be declared a synonym of *Plesiosorex*, because for the present it is difficult to differentiate the two genera morphologically. We hope that we soon will know more about these relationships because some North American collections contain extensive unpublished material, possibly permitting determination of the phylogenetic lineages from *P. coloradensis* to the latest forms of the Upper Pliocene.

The known diversity of the subfamily Heterosoricinae has greatly increased in the last 15 years. Although new North American and European species have been described, their phylogenetic affinities still are not clearly understood. Several authors oversimplified this problem by considering all later forms to have descended from earlier ones. Their nice phylogenetic trees hardly show real phylogenetic relationships. Typical examples are the cases of *Saturninia* and *Dinosorex huerzeleri* (=*Heterosorex* aff. *neumayrianus*) from Rickenbach, which, being the oldest known forms, are used and abused as ancestors for all sorts of groups. Among the present abundance of known heterosoricines there are hardly two species of different age that can be derived with certainty from one other. The conclusions obtained by observing the trends of one feature always seem to be opposed by those from other features. Their systematics are also complicated by the fact that many of the taxa are incompletely known, for example from one fragmentary mandible—and by and large differ very little. The latter can probably be explained in the following manner: the Heterosoricinae (analogous to the rodents) specialized very early—probably already in the Eocene—and apparently very successfully too; this specialization considerably limited their spectrum of evolutionary possibilities, whereas in return, as in rodents (Wood, 1947), increased their chances for parallel evolution. In the Miocene of Europe and North America there are a great number of different evolutionary lines, often very hard to distinguish. The diversity of taxa in the Oligocene of both continents also argues in favor of the existence of different lineages. Therefore, the phylogeny of this group is at present unclear.

The relationships between North American and European heterosoricines are also unresolved and these taxa are compared below.

Comparisons of Oligocene Heterosoricines of America and Europe

The Oligocene soricid faunas of North America are dominated by the genus *Domnina* Cope, 1873, of which five species have been described. After the Middle Oligocene (Orellan) other forms, distinctly different from *Domnina*, occur. These are here provisionally designated as *Pseudotrimylus* Gureev, 1971 (see below for detailed discussion of the nomenclature). In the European Oligocene two genera of heterosoricines are distinguishable—*Quercysorex* Engesser, 1975, and *Dinosorex* Engesser, 1972. These will be discussed later.

Differences between Domnina *and the Oligocene* Pseudotrimylus.[7]—The Oligocene *Pseudotrimylus* (the only known specimens are those of *P. compressus* from Cedar Creek and Pine Ridge [see Repenning, 1967:Fig. 5] and that of *Pseudotrimylus* sp. from Lawson Ranch; see Fig. 2b and Plate 7d) differs from *Domnina* in its stouter mandible; its lowest point is immediately behind M_3 and its height increases distinctly anteriorly. The mandibular height of *Domnina* is about the same from front to back, except that below M_1 a gentle inlet can be

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[6] As far as the problematic nature of the names *Heterosorex* and *Trimylus* is concerned, see Engesser (1975).

[7] For use of the name *Pseudotrimylus* see p. 15.

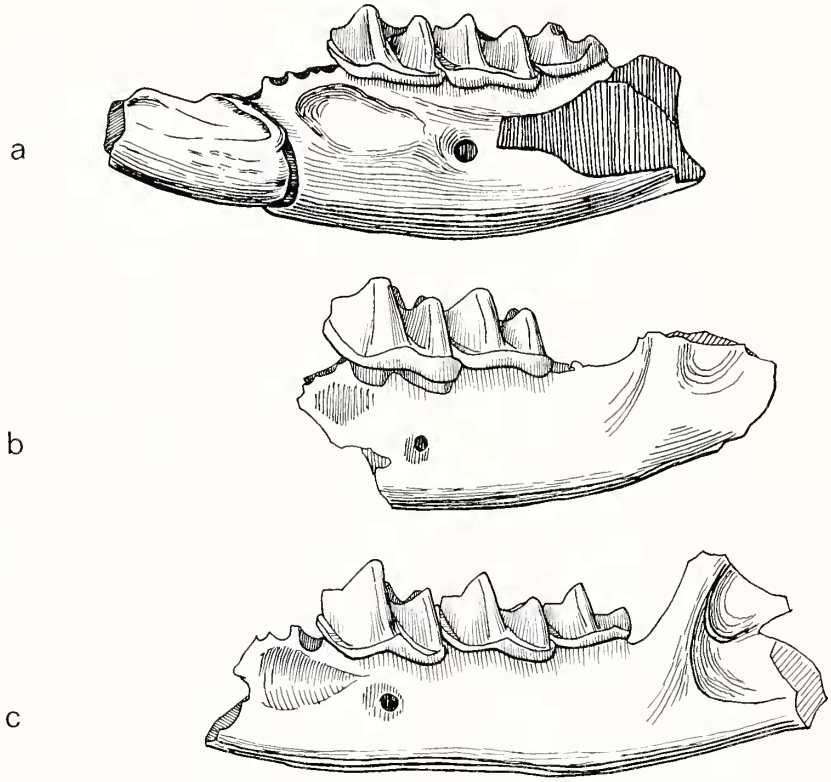

Fig. 2.—a) *Dinosorex huerzeleri* (Engesser), L mandible with I, M_1–M_3, (type) MO, Rb. 101, Rickenbach (Canton Solothurn, Switzerland), Late Oligocene; b) *Pseudotrimylus* sp., L mandible with M_1–M_2, CM 10922, Lawson Ranch, Goshen Co., Wyoming, Lower Orellan?; c) *Domnina* sp., L mandible with M_1–M_3, CM 10403, Pipestone Springs, Jefferson Co., Montana, Chadronian. All figures 8×.

observed (Fig. 2c). The last antemolar of *Domnina* is largest, whereas in *Pseudotrimylus* the first is largest. The M_1–M_2 of *Domnina* are of equal size, and have slender, pointed cusps with the protoconid highest (Plate 7e). In *Pseudotrimylus* the lower molars decrease in size posteriorly and are more squat than in *Domnina,* with the protoconid only slightly higher than the other cusps. The hypocristid in all species of *Domnina* extends behind the entoconid (Modus B, Engesser, 1972:76), whereas in *Pseudotrimylus* it mostly joins the entoconid (Modus A). Finally, the teeth of *Domnina* are intensely pigmented, whereas those of *Pseudotrimylus* are either not at all (for example, *Pseudotrimylus* from Lawson Ranch) or only slightly pigmented (*P. compressus*). (For more differences, see Repenning, 1967:10.)

Domnina *and* Quercysorex.—Crochet (1968), noting the great similarity between *Domnina* on the one hand and "*Amphisorex*" *primaevus* Filhol from the Quercy and "*Sorex*" *herrlingensis* from Herrlingen on the other, placed the two European forms and the Rickenbach soricid in the American genus *Domnina.* However, later comparisons (Engesser, 1975) of the three European taxa with different species of *Domnina* illustrated that they differed in some important features, and that their similarities were due to common retention of primitive features. Consequently, the genus *Quercysorex* was erected (Engesser, 1975) for the shrews from the Quercy and Herrlingen. The Rickenbach form (Plate 7c and Fig. 2a), which in my opinion does not resemble *Domnina,* was referred to a new species—*D. huerzeleri*—in the genus *Dinosorex.*

Pseudotrimylus compressus *and* Dinosorex huerzeleri.—This Oligocene species of *Dinosorex* shows more similarities with the Oligocene *Pseudotrimylus* of North America (for example, *P. compressus*)—the massive horizontal ramus of the mandible and the inflated, low crowned lower molars (see Fig. 2a and Plate 7c). Nevertheless, there are also important differences—*Dinosorex* is much more primitive with five antemolars and a hypocristid extending behind the entoconid (Modus B);

Table 1.—*Comparisons of American and European Heterosoricinae (except for such primitive forms as* Domnina *and* Quercysorex*).*

Characters	Typical for North American forms	Typical for European forms
Position of the mental foramen	below M_1; exception: *P. roperi*	below M_2 or below the space between M_1 and M_2
Pigmentation	tooth apices unpigmented; exceptions: *P. compressus* *P. mawbyi*	distinct pigmentation of tooth apices
Mesostyle of the upper molars	undivided; exceptions: *Heterosorex* sp. (Quarry A), *Paradomnina*	divided
Hypocone of M^1 and M^2	very well developed	much weaker
Posterior labial cusp of P^4	very well developed (*P. mawbyi*!)	very weak or lacking
Course of the posterior crest of the hypoconid of M_1 and M_2 (hypocristid)	directly to the entoconid (Modus A); exceptions: *P. dakotensis*, possibly *Paradomnina*	behing the entoconid, often separated from this cusp by a small valley (Modus B); exceptions: *Dinosorex zapfei* from Neudorf and Vermes
Proportions of M_1 and M_2	M_2 comparatively small; exception: *Paradomnina*	M_2 comparatively large; exception: *Dinosorex*, *Pachygnathus*

P. compressus is derived in that only three antemolars occur and the hypocristid joins the entoconid directly (Modus A). In addition, the mental foramen in *Dinosorex* is situated below the trigonid of M_2, whereas in *P. compressus* it is below M_1.

The Miocene Heterosoricinae

In a revision of the European Heterosoricinae (Engesser, 1975), I proposed suppression of the poorly defined genus *Trimylus* Roger, 1885. *Heterosorex* Gaillard, 1915, on the other hand, is very well defined. However, the type species of the latter—*H. delphinensis* from La Grive—shows many morphological peculiarities (for example, the hardly divided *fossa masseterica* on the mandible), shared only by *H. neumayrianus* among known heterosoricines. Therefore, the genus *Heterosorex* should be limited to the species *H. delphinensis* and *H. neumayrianus* (for the new diagnosis of *Heterosorex*, see Engesser, 1975). All other European species hitherto included in *Heterosorex* or *Trimylus* were referred to the genus *Dinosorex*, for which I gave an emended diagnosis.

North American Miocene Heterosoricinae seem to be more diverse than those from the Miocene of Europe. Such extremely specialized North American forms as *Ingentisorex* and *Pseudotrimylus mawbyi*, and such primitive ones as *Paradomnina* have no corresponding forms in Europe. As noted by different authors, there is no difficulty in morphologically distinguishing most of the latter from European taxa. However, among the New World shrews one is out of place—*P. roperi* from Quarry A shows similarities in some features to the European heterosoricines, especially *Dinosorex zapfei* from Neudorf (see Engesser, 1975).

Apart from *Ingentisorex* and *Paradomnina* all other North American Miocene species without exception were classified as *Trimylus* or *Heterosorex*. Because *Trimylus* is invalid and because *Heterosorex* has been redefined to include only the two European species *H. delphinensis* and *H. neumayrianus*, to which genus do these North American Miocene shrews belong? Gureev (1971) introduced *Pseudotrimylus* for "*Heterosorex*" *roperi* from Quarry A. However, as already mentioned, the Quarry A form is out of place among American soricids. Also, the taxa hitherto placed in the genera *Heterosorex* and *Trimylus* are very heterogeneous. Nevertheless, I abstain from introducing a new genus at this time and provisionally use the generic name *Pseudotrimylus* for all North American forms except *Domnina*, *Paradomnia*, and *Ingentisorex*.

Comparison of Miocene Heterosoricinae of Europe and North America

Considering the diversity of heterosoricines on both continents, it is remarkable that no general feature distinguishes among forms from America and Europe.

Position of the mental foramen.—With one exception (*P. roperi*), the mental foramen in all known North American Heterocoricinae is situated below M_1. In all European taxa, except for *Quercysorex*, it occurs more posteriorly, either below M_2 or below the interspace between M_1 and M_2 (Table 1 and

Plate 8). The position of this foramen is one of the most important systematic features because, as different investigations showed, it is remarkably stable within populations and species. According to Stehlin (1940), a more posteriorly placed foramen in soricids is more evolved than a more anteriorly placed one, because it indicates the presence of a large incisor. This observation, certainly correct in vaster connections, does not apply to the subfamily Heterosoricinae. For example, the mental foramen in species with relatively small lower incisors, such as those from Rickenbach, Wintershof-West, and Vieux Collonges, is not placed more anteriorly than in those showing a large incisor (species from Anwil, Sansan, Neudorf).

Pigmentation.—The use of pigmentation of fossil soricid teeth as a diagnostic feature is still controversial. In certain cases it cannot be stated with certainty whether fossil teeth showing no pigmentation were formerly pigmented or not. Teeth of known European Heterosoricinae, except *Quercysorex,* are pigmented. American heterosoricines, on the other hand, show no pigmentation except for *Domnina* which has heavily pigmented cusp apices, and *P. mawbyi* and *P. compressus,* which possess slightly pigmented teeth (see Table 1).

Mesostyle of the upper molars.—In all European species known to me, the mesostyle of M^1, and in a smaller measure also of M^2, is more or less divided. In American heterosoricines such a division generally does not occur (see Plate 6). In Wilson's (1960) "*Heterosorex* sp.," the mesostyle is more nearly divided than in any European shrew. This shrew still is so aberrant in this feature and in others—its upper molars also show a well-developed mesocone—that it is of no account to our investigations. According to Hutchison (1966) the mesostyle on the upper molars of *Paradomnina* is also slightly divided.

Direction of the posterior crest of the hypoconid (hypocristid) relative to the entoconid.—In Europe and North America both orientations of the hypocristid branch occur (Modus A and B, Engesser, 1975). Among European heterosoricines (*Quercysorex,* most species of *Dinosorex, Heterosorex*) the indirect course (Modus B) is far more common, whereas in American species the indirect course is more common, excluding *Domnina, Paradomnina,* and *Ingentisorex* from these comparisons (see Table 1). As Repenning (1967) noted, both modi represent different stages in an evolutionary trend, with Modus B the more primitive. Modus A occurred in America much earlier (Middle Oligocene [Orellan, in *P. compressus*]), than in Europe (Middle Miocene [NMU 6 with *Dinosorex zapfei* from Neudorf a.d. March]). With the exception of the aberrant *Ingentisorex* and *Paradomnina,* I do not know any Miocene heterosoricine from North America with Modus B. In Europe, on the other hand, heterosoricines with Modus B occur throughout the Miocene.

Proportions of M_1 compared with those of M_2.—Another distinctive feature appears to be the proportions of the M_1 and M_2—in American heterosoricines except *Paradomnina* and *Domnina,* M_2 is smaller than M_1; in European taxa there is generally less difference in size between M_1 and M_2 (Plate 7). This distinction is obvious in very early forms on both continents (for example, between *P. compressus* and *Dinosorex huerzeleri* from Rickenbach [Plate 7c and d]).

Comparisons of Pseudotrimylus roperi *with European Forms*
(see also Wilson, 1960; Doben-Florin, 1964)

As mentioned above, of all known North American heterosoricines *P. roperi* from Quarry A is the most similar to European forms. This fact led several authors (Doben-Florin, 1964:70; Thenius, 1969:135) to consider *P. roperi* either as an immigrant from Europe or the ancestor of many Miocene European heterosoricines (for example, *D. sansaniensis*). *P. roperi* cannot be the ancestor of *D. sansaniensis* despite many features in common. On M_1 and M_2 of *P. roperi,* the hypocristid runs directly to the entoconid (Modus A, Plate 7a), a more evolved condition than in *D. sansaniensis,* which still shows an indirect course of the hypocristid on M_1 and M_2 (Modus B, Plate 7b). Thus, in all probability, the two species belong to two different evolutionary lines.

As far as *P. roperi* being a European element within the American Heterosoricinae is concerned, we have little evidence. *P. roperi* has a number of features in common with American forms, in which it differs from European ones—(1) the tooth apices of *P. roperi* do not seem to be pigmented[8], whereas, except for *Quercysorex,* all European heterosoricines known to me have pigmented teeth; (2) the mesostyle on the upper molars of *P. roperi* is un-

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[8] Wilson's assumption that the teeth of *P. roperi* were originally pigmented (1960:28) is based, as of this writing, on analogy to the pigmentation of *D. sansaniensis.*

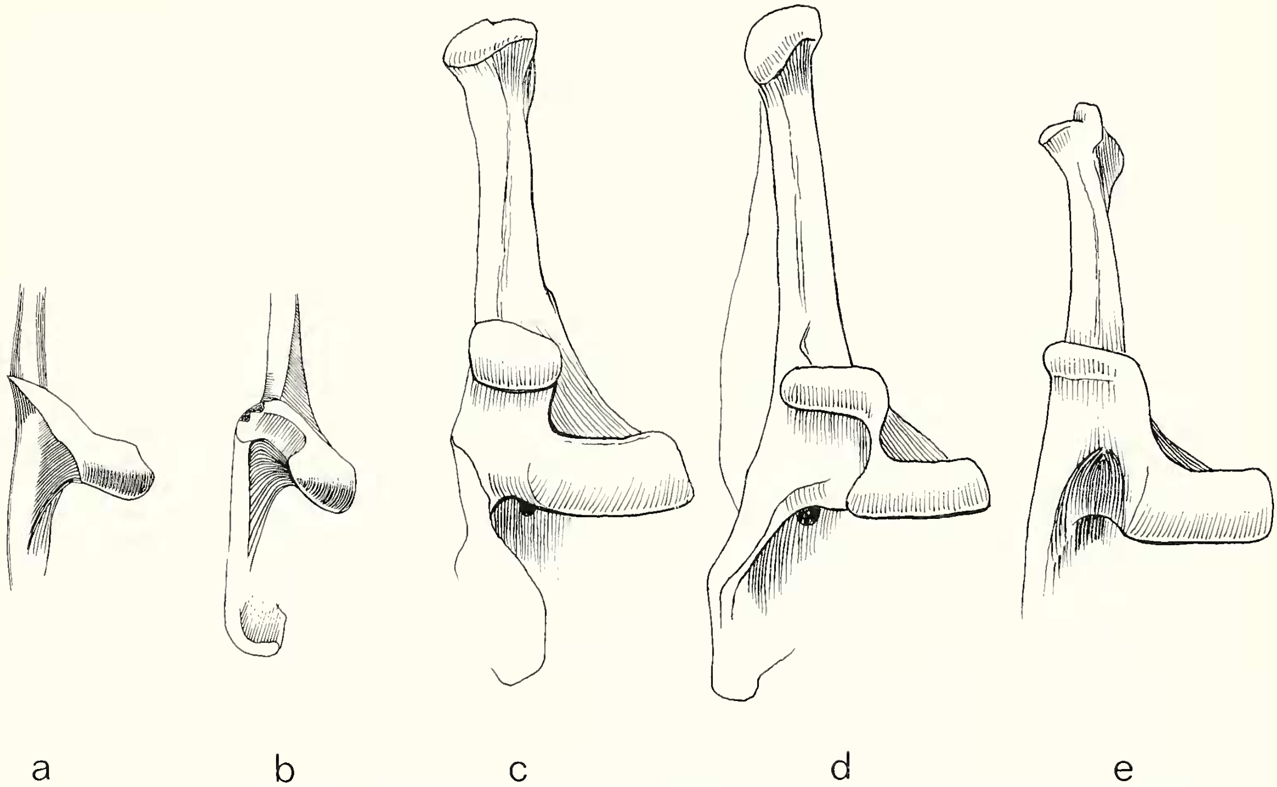

Fig. 3.—Left mandibular condyle of a) *Domnina thompsoni* Simpson (after McDowell 1958); b) *Quercysorex primaevus* (Filhol); c) *Dinosorex sansaniensis* (Lartet); d) *Dinosorex zapfei* Engesser; e) *Pseudotrimylus roperi* (Wilson). All figures ca. 10×.

divided[9], whereas mesostyle division occurs in all European heterosoricines for which the upper dentition is known (see Plate 6); (3) the hypocone of M^1 and M^2 is much more developed in *P. roperi* than in any European form (Plate 6b); (4) the posterolingual cusp on P^4 is strong in the American species, but much weaker or lacking in European species. With the stocky shape of the teeth and M_1 much larger than M_2 compared to European forms, *P. roperi* resembles American *Pseudotrimylus*. In addition, there seems to be no morphological impediment to deriving *P. roperi* from certain Oligocene North American heterosoricines, such as *P. compressus*; similarly, in my opinion, the Miocene European heterosoricines can be easily derived from Oligocene representatives of the group, such as *Dinosorex huerzerleri* of Rickenbach (Stampian). The authors not considering *P. roperi* as a European immigrant were probably influenced in their opinion by the position of the mental foramen.

However, the posterior migration of the mental foramen can occur on forms of different continents as a parallel development.

Parallel Developments and Analogous Trends in North American and European Heterosoricinae

Some new morphological acquisitions observed on both sides of the Atlantic cannot be explained by a faunal exchange between North America and Europe after the Eocene, unless one assumes continuous traffic in both directions across the Bering Strait. In my opinion, these "migrations" must be regarded as exceptions (see Discussion). An example of these, probably parallel, developments, is the gradual division of the mandibular condyle, which occurred on both continents. The American Heterosoricinae apparently developed this division earlier than the European shrews. *Pseudotrimylus dakotensis* from the middle Arikareean already shows a distinctly divided condyle (Repenning,

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[9] It is not certain that the mesostyle on the upper molars of *P. roperi* was not divided, because as far as I know there is no known unworn upper molar of this animal. However, in European heterosoricine upper molars the division of the mesostyle can often also be observed in relatively worn teeth, especially in labial view. So, the conclusion of an undivided mesostyle in *P. roperi* seems justified.

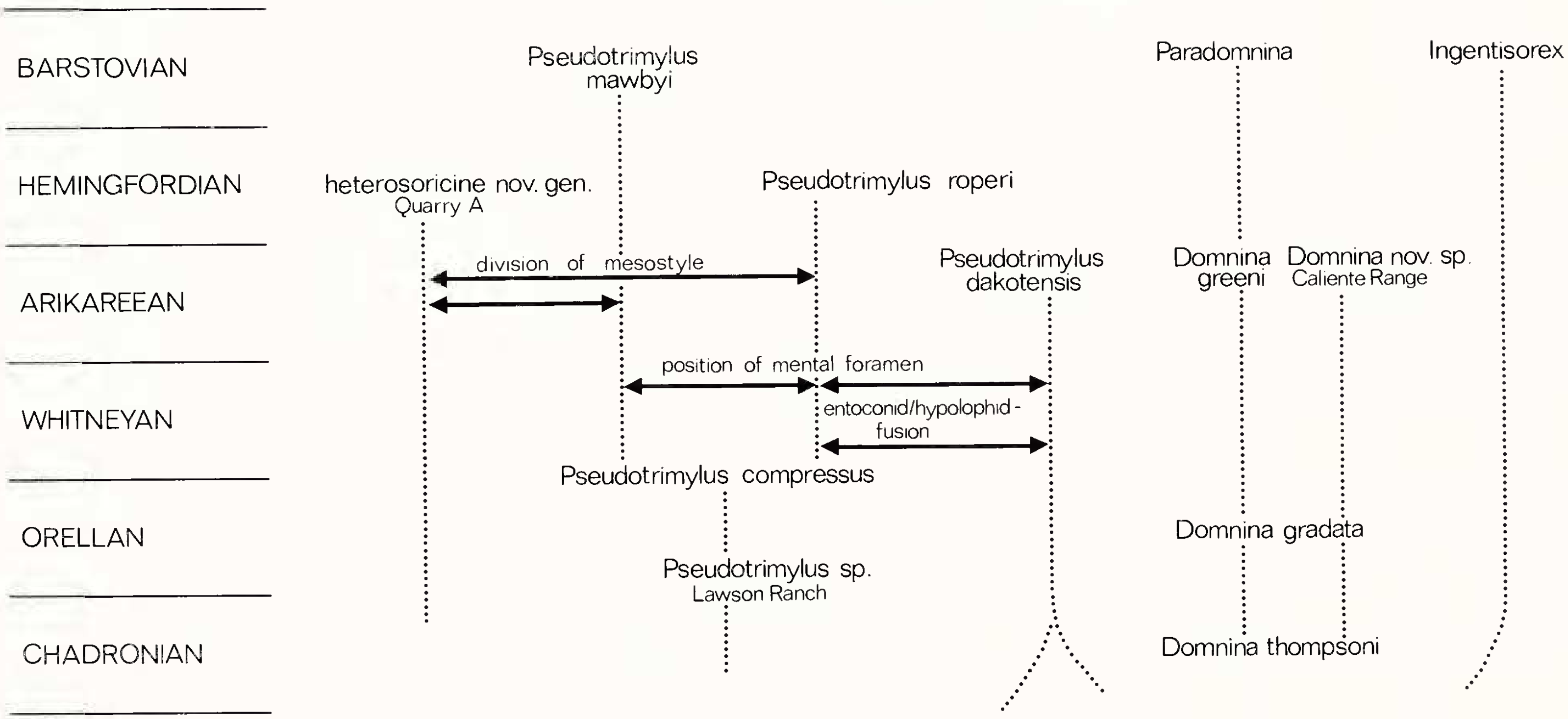
BARSTOVIAN
HEMINGFORDIAN
ARIKAREEAN
WHITNEYAN
ORELLAN
CHADRONIAN
Pseudotrimylus mawbyi
heterosoricine nov. gen. Quarry A
Pseudotrimylus roperi
division of mesostyle
Pseudotrimylus dakotensis
position of mental foramen
entoconid/hypolophid - fusion
Pseudotrimylus compressus
Pseudotrimylus sp. Lawson Ranch
Paradomnina
Ingentisorex
Domnina greeni
Domnina nov. sp. Caliente Range
Domnina gradata
Domnina thompsoni

Fig. 4.—Table of suggested morphological relations of some North American Heterosoricinae. Vertical dotted lines mean only that according to our present knowledge there is no morphological hindrance against a derivation of one form from another. Characters making a derivation impossible are represented as horizontal arrows. For the European forms see Engesser, 1975.

1967:Fig. 6), whereas that of the "Burdigalian" (NMU 3) *Heterosorex neumayrianus* from Wintershof-West, besides *Quercysorex* the first European form, of which the condyle is known, is still undivided. The Middle Miocene (NMU 6) *Dinosorex* from Neudorf shows a more distinct separation of the articular faces, which are still coherent (Fig. 3). Probably in European forms the division of the condyle was independently acquired in two different lines since such an early species as *Quercysorex primaevus* shows a more advanced stage of condylar division than the more recent *Heterosorex neumayrianus*. The modern Soricinae developed a divided mandibular condyle completely independently from these phenomena in Heterosoricinae.

The increase in fusion of the hypocristid with the entoconid in lower molars probably also developed independently on both continents. This process probably occurred twice, in North America and in Europe, in two different evolutionary lines—in North America, in the Orellan or earlier *Pseudotrimylus compressus* and in the Late Miocene *Paradomnina* (see Fig. 4); in Europe *Dinosorex zapfei* from Neudorf (Middle Miocene NMU 6) is the first heterosoricine with a Modus A connection. A renewed tendency towards developing a Modus A connection is displayed by the Late Miocene *Dinosorex* from Can Llobateres (NMU 9). Another trend, which can be observed on both sides of the Atlantic, is the increase in massiveness of the mandible. This bone is very slender in primitive forms such as *Quercysorex* and *Domnina*, increases gradually in massiveness and reaches extraordinary robustness in the geologically youngest forms such as *Pseudotrimylus mawbyi* and *Dinosorex pachygnathus*. This increase in massiveness of the mandible is accompanied by the increase in size of the lower incisor, which reaches its largest dimensions in the two latter forms.

LIMNOECUS

(Family Soricidae Gray, 1821)

Several authors (R. W. Wilson, James, Doben-Florin, Baudelot) considered some small soricids from European localities to represent the American subfamily Limnoecinae (Repenning, 1967). This assignment is very doubtful because of the poor documentation and paucity of material. For example, among American forms, the upper dentition is not known.

The European forms repeatedly assigned to the Limnoecinae are "*Limnoecus*" *micromorphus* Doben-Florin from Wintershof-West, "*Limnoecus*" *grivensis* Depéret from La Grive, "*Limnoecus*" *dehmi* Viret and Zapfe from Vieux Collonges, and *Paenelimnoecus crouzeli* from Sansan.

Doben-Florin (1964) assigned the species from Wintershof-West to *Limnoecus* mostly because of the slightly developed entoconid on the lower molars and the unicuspid talonid of M_3. Chiefly because of the structure of the last lower antemolar (P_4?; "antemolars" are teeth between incisor and M_1, "Zwischenzahne" of Doben-Florin), Repenning (1967:23–24) opposed this assignment and united this shrew with the Crocidurinae? *incertae sedis*. He also considered the distance between the protoconid and metaconid in the species from Wintershof-West to be too large for a limnoecine.

Sorex grivensis and "*Sorex*" *dehmi* (Viret and Zapfe, 1951) were also incorporated in *Limnoecus* (James, 1963). According to James all small Tertiary soricids from Europe (possibly including *Sorex antiquus* Pomel) should be referred to *Limnoecus*, based on the similarities of the mandible (undivided condyle, large, triangular pterygoid fossa) and tooth structure (reduced talonid of M_3, molar protoconid and metaconid close to one another, and others). *Limnoecus* is thus very broadly interpreted and unites almost all species that cannot be assigned to *Crocidura* or *Sorex*. Repenning (1967) defined the genus *Limnoecus* more strictly, placed *Miosorex grivensis* and "*Sorex*" *dehmi* in the subfamily Crocidurinae, and included only two species in *Limnoecus*—*L. tricuspis* Stirton and *L. niobrarensis*. *Sorex vireti* was referred to a new genus, *Angustidens*, which, together with *Limnoecus*, was placed in the Limnoecinae. The determining factor for Repenning's classification was the structure of the last lower antemolar (P_4?) and M_3, the pigmentation and the position of the mental foramen.

I concur with Repenning's reasoning just to include the mentioned European forms in *Limnoecus* or in the Limnoecinae. *Limnoecus*, interpreted as broadly as James did, becomes a "wastebasket-genus," in which all forms not identified as either *Crocidura* or *Sorex* are assembled. The arguments by which Repenning excludes *Miosorex grivensis*, "*Sorex*" *dehmi*, and "*Limnoecus*" *micromorphus* from the subfamily Limnoecinae seem convincing to me. Although Baudelot (1972:100) adopted Repenning's definition of the subfamily Limnoecinae—a strong entoconid on the lower molars—at the same time (and on the same page!) she character-

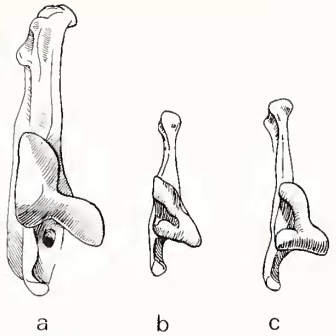

Fig. 5.—Right mandibular condyle of a) *Paenelimnoecus crouzeli* Baudelot, NMBS, Ss. 1002, Sansan, France, Middle Miocene, 12.5×; b) *Limnoecus niobrarensis* Macdonald, (after Repenning 1967) Nebraska, Barstovian, 5×; c) *Angustidens vireti* (Wilson), (after Repenning 1967) Quarry A, Hemingfordian, 5×.

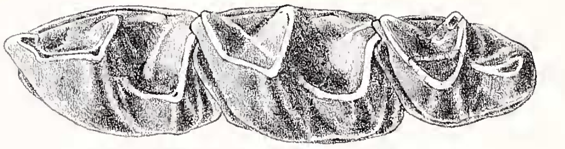

Fig. 6.—*Paenelimnoecus crouzeli* Baudelot, LM$_1$–M$_3$, NMBS, Ss. 6706, Sansan (France), Middle Miocene, 25×.

ized the new genus *Paenelimnoecus* by the loss of the entoconid. Besides the loss of the entoconid, the species from Sansan shows other differences from American Limnoecinae, the most important one being in the structure of the mandibular condyle—the condyle of *Paenelimnoecus* (see Fig. 5a) does not show any "labial emargination" as is typical in the Limnoecinae (Repenning, 1967:4), but a "lingual emargination," generally characteristic for the Soricinae. In addition the horizontal part of the condyle is distinctly wider in *Paenelimnoecus* compared to that of the Limnoecinae. This condylar structure implies the soricine affinities of *Paenelimnoecus*. This tiny shrew from Sansan also shows other differences from American soricids—the coronoid process is distinctly higher; the mental foramen is located somewhat more posteriorly; the lower molars and the last antemolar (P$_4$?) have a lingual cingulum, lacking in American soricids (see Fig. 6); the angle of the trigonid of M$_1$ is more open than in Limnoecinae. Finally, there is the problem of pigmentation—of the seven jaw fragments of *Paenelimnoecus crouzeli* in the Basel collection, none shows pigmentation. Because the enamel in this species is so delicate, the cavity at the base of the teeth appears through the enamel, with the effect that the tops of the teeth appear differently colored than the base. Because of this I stated (1972:66) that the teeth of soricid A from Sansan (=*Paenelimnoecus crouzeli*) might have originally been pigmented. I have not seen Baudelot's specimen, but it seems strange that only this specimen should show pigmentation, whereas seven others from the same locality do not. If *Paenelimnoecus* actually does not show any pigmentation of the teeth, this would be one more reason for separating it from the Limnoecinae.

It seems that for the present there is no reason to assign any of the European soricids treated here with the Limnoecinae.

RELATIONSHIPS OF RODENTS

"SCIUROPTERUS"
(Family Sciuridae Gray, 1821)

History of Investigations

Fossil flying squirrels have been known for a long time. In the last century a number of European forms were described as different species of *Sciurus*, but it was not until 1893 when Major connected these finds with flying squirrels. From that time all sciurid teeth showing secondary ridges and crenulated enamel were united in the genus *Sciuropterus*. The numerous Recent flying squirrels were split into different genera much earlier, although they resemble each other to some extent more than many fossil forms. This difference in treatment was perhaps motivated by the fact that this classification of Recent forms was based not only on the dentition but also on other morphological features (skeleton, color of the fur, and others). On the other hand, only the dentition of the fossil flying squirrels was known. The scarcity of remains of flying squirrels, although known from most Miocene localities of Europe, seems to be an additional reason why these animals were for so long united in the collective genus "*Sciuropterus*." Mein (1970) divided the former genus *Sciuropterus* into four genera—*Cryptopterus*, *Forsythia*, *Miopetaurista*, and *Pliopetaurista*. The latter two names were introduced by

Kretzoi (1962), but because this author did not give any diagnosis for these names, they were regarded as *nomina nuda*. Henceforth, the name "*Sciuropterus*" must be regarded as a synonym of *Pteromys*, the common Recent flying squirrel.

For a long time no Tertiary flying squirrels were known from America. James (1963) described two forms from the Barstovian and Clarendonian of the Cuyama Valley, which he called *Sciuropterus mathewsi* and *S. uphami*. Also from the Upper Miocene (Barstovian) Shotwell (1968) reported two isolated teeth, found in the Red Basin of Oregon and determined as *Sciuropterus* sp. Lindsay (1972) introduced two new species, *S. jamesi* and *S. minimus*, for remains from the Barstow Formation in California.

James (1963) pointed out that remains of flying squirrels from the Cuyama Valley did not show a great similarity with the Recent *Glaucomys* of North America. Instead he saw similarities between North American dentitions and those of fossil flying squirrels from Europe. He saw two possible explanations for the phylogenetic relationships of his finds—a faunal exchange with Europe, thus origin from European forms, or a descent from certain Early Tertiary paramyids from North America, showing cheek teeth with crenulated enamel. James preferred the former possibility. Shotwell (1968) doubted if the two teeth from the Red Basin really represent flying squirrels and referred to the occurrence of a similar tooth pattern in paramyids and *Marmota nevadensis*.

The earliest fossil flying squirrels are known from the Lower Miocene of Europe. The earliest American remains generally considered as flying squirrels are from the Upper Miocene. This fact led different authors to see the European forms as ancestors for the American and to postulate a Miocene "migration" of flying squirrels from Eurasia to North America.

Regarding this interpretation I have some doubts. First, in addition to numerous morphological similarities between the forms from both continents (see Mein, 1970:33), there are some important differences that make it impossible to trace the American species back to any known form. In the following I will go into details of these differences. Therefore, if one wants to adhere to the migration theory, one is compelled to postulate a hypothetical Eurasian ancestor.

In addition, it can be assumed that in analogy to Recent flying squirrels, the fossil ones were forest-dwellers. Remains of fossil flying squirrels are found frequently in lignite deposits (Göriach, Viehhausen, Anwil). However, it is not known whether they had already developed a patagium and were able to glide from tree to tree. Moreover, the Miocene flying squirrels were probably living in a tropical or subtropical climate. We have many indications for such a climate in the Miocene of Europe, and also James (1963:19) suggests a Neotropical ecotone for the Cuyama Badland in the Neogene. Also most species of Recent flying squirrels are living in the tropics (*Glaucomys* and *Pteromys* seem to be exceptions). Such dwellers of tropical or subtropical forests may well be dependent upon special ecologic conditions. Therefore, it is difficult to imagine that such animals had spread over great distances, without encountering any climatic or ecologic barrier. In Miocene times, the only possible route between Eurasia and North America seems to have been a land bridge across the Bering Strait, but as Simpson (1947:14) pointed out and later authors confirm (see Beringia History, 1973), there is no evidence that there was ever a tropical or subtropical climate on this land bridge.

Mein (1970), in his study of the fossil flying squirrels from western Europe, concluded that not even within this relatively small area was there a lively faunal exchange. He suggests a polyphyletic origin for the three groups he distinguished.

As an alternative to the "migration" theory explaining the dental similarities of forms from both continents, the possibility of parallel evolution seems more realistic to me. In this case, parallel evolution seems even more probable because, as has been mentioned several times, the whole group of fossil flying squirrels is defined exclusively on the dentition. Sciurid-like teeth showing enamel crenulations usually are assigned to flying squirrels. The fact that such teeth should not automatically be assigned to flying squirrels is shown by the fact that similar teeth are also known from completely different groups (for example, paramyids *Thisbemys* and *Paramys*).

In discussion with colleagues about intercontinental faunal relationships I heard several times: "forms whose ancestors we do not know and which suddently appear in a layer represent without doubt immigrants." In my opinion this point of view greatly overestimates the actual state of our knowledge. True, in the case of the fossil flying squirrels of North America it is strange that no form from an earlier level than Barstovian is known. However, going further back in stratigraphy, one definitely encounters forms coming into question as possible ancestors of the American "sciuropteres." As already mentioned, James considered a direct extraction of the American "sciuropteres" from certain paramyids, as an alternative to the derivation from European species (*Cryptopterus* from Wintershof-West). As common features between these paramyids and the Californian "sciuropteres" James pointed out especially the subdivided lophs, the "accessory loph" and the hypocone of the upper molars distinctly separated from the protocone.

I was very surprised by the flying squirrel-like dentition of some species of *Prosciurus* (see Plates 9 and 10). Upper premolars and molars of many species of *Prosciurus* show well-developed proto- and metaconules and distinct incisions in front of and behind the protocone, otherwise typical for flying squirrel teeth. In addition, the teeth of many *Prosciurus* species show a distinct crenulation. Furthermore, some *Prosciurus* species show features typical of the Late Tertiary "*Sciuropterus*" of North America—the long mesoconid, extending almost to the labial margin of the tooth and the isolated mesostylid of the lower molars. In the formation of the masseteric fossa on the labial side of the mandible I found a surprising resemblance, the systematic significance of which I cannot evaluate—a fragment of a *Prosciurus* mandible from Pipestone Springs (CM 9321) shows the same deeply engraved, anteriorly rounded fossa as "*Sciuropterus*" *mathewsi* from Cuyama Valley (see James, 1963:Fig. 37a). The mandibles of other sciuropteres known to me from the Old World show a much less deep (*Petaurista, Petinomys*) and anteriorly more tapered (*Miopetaurista, Iomys, Pteromys, Hylopetes*) masseteric fossa.

Also in the European Eocene and Oligocene there are rodents showing a great similarity to Late Tertiary sciuropteres. Several authors already referred to these resemblances. Thus, Schlosser (1884), for example, pointed out the far-reaching morphological correspondences of *Sciurodon* from the Quercy with the Recent *Pteromys*. Major (1893) emphasized the similarities of *Sciuroides* and *Pseudosciurus* on the one hand and *Sciuropterus* (*Iomys*) *horsfieldi* and *Sciuropterus* (*Belomys*) *pearsoni* on the other hand. To this list I would add *Plesiospermophilus* from the Phosphorites, whose molars, especially the lower, might be determined as belonging to a sciuroptere if found in a Late Tertiary deposit (see Plate 10).

In total, in North America as well as in Europe there are throughout the Early Tertiary forms known which, based on our present knowledge, cannot be excluded from the ancestry of the Miocene forms, even though separated from the latter by a long period. Therefore, it is quite possible that the Late Tertiary American and European rodents with flying squirrel-like dentition developed completely independently from each other, with the European Miocene forms, for example, having originated from *Plesiospermophilus*, the American from *Prosciurus*. However, our present knowledge is too fragmentary to determine definitely an ancestral group. I only want to show that in both continents there are known Early Tertiary forms that might have been ancestors of the later ones, without the necessity of a Miocene migration. At any rate, as an attempt to explain the striking similarities of North American and European "*Sciuropterus*," parallelism seems to me more probable than "migration." In this opinion I am supported by the results obtained by Gorgas (1967) who, investigating Recent Petauristinae, showed that the Recent flying squirrels do not represent a homogeneous group. Thus *Glaucomys*, for example, corresponds in the digestive tract with the Sciurinae rather than the Petauristinae. Hence, possibly the Recent flying squirrels also represent a polyphyletic group.

The generic name *Sciuropterus* has here been put in quotation marks for two reasons. First, it seems possible that the "*Sciuropterus*" from California have nothing to do with flying squirrels, but perhaps with rodents of a completely different group having adapted their dentition to a similar manner of feeding. (Maybe they are not even sciurids!) Thus, many authors (McGrew, 1941; Stock, 1935; Wilson, 1949; Wood, 1962; Rensberger, 1975) have connected *Prosciurus*, in spite of its flying squirrel-like dentition, not with the Sciuridae but rather with the Aplodontidae.

The second reason is the following: as mentioned above, Mein (1970) in his study of the Neogene flying squirrels from western Europe divided the genus "*Sciuropterus*" into four genera, and the name "*Sciuropterus*" is only a synonym of *Pteromys*. The four "*Sciuropterus*" species from California ("*S.*" *uphami, mathewsi, jamesi*, and *minimus*) in my opinion represent a homogeneous group that cannot be connected to any European genus. Therefore, I propose to separate them as a particular genus, which I would call *Petauristodon*. This separation is based on morphological differences and not on the above-mentioned doubts about the possibilities of an intercontinental dispersal.

Petauristodon, new genus

Derivatio nominis.—Petauristodon:Petaurista tooth-like; this name is intended to refer to the similarities of the teeth of this genus with those of flying squirrels. Thus, it is left open if *Petauristodon* is really a flying squirrel or not.

Diagnosis.—Cheek teeth of a sciuroid pattern, flying squirrel-like, with crenulated enamel. Upper P and M—with distinct proto- and metaconules, well developed mesostyle; in some specimens hypocone distinctly separated from the protocone; "accessory loph" between proto- and metaloph always present, often also an accessory loph in the first syncline starting from the protocone; M^3 as far as known (*P. uphami* and *P. minimus*) without metaloph. Lower P and M—with short metalophid, isolated mesostylid, long mesoconid mostly reaching to the tooth margin, without any "anterosinuside" (Mein); enamel more crenulated than that of the upper teeth.

Type species.—P. mathewsi James, 1963.

Type locality.—Remnant Hill, UCMP loc. V-5663, Cuyama Valley, California.

Stratigraphic range.—Barstovian to upper Clarendonian.

Included species.—P. uphami James; *P. mathewsi* James; *P. jamesi* Lindsay[10]; *P. minimus* Lindsay.

Differential diagnosis.—From *Miopetaurista, Petauristodon* differs in the following features: in the mesostyle, the "accessory loph," and the distinct hypocone of the upper molars; the lack of a spur extending backward from the metaconule on M^3; in the isolated mesostylid, the short mesolophid and the large mesoconid, reaching to the tooth margin on the lower molars.

From *Cryptopterus, Petauristodon* is different in smaller size; on the upper molars better developed proto- and metaconule, the shorter distance of the lophs from each other at their point of attachment to the protocone; on the lower molars by: the lack of an "anterosinuside" (Mein) and the long mesoconid.

From *Forsythia, Petauristodon* is different in the distinct mesostyle and the well developed "accessory loph" of the upper molars; by the lack of lateral compression of M_1 and M_2, typical for *Forsythia,* by the isolated mesostylid and the long mesoconid of all three lower molars.

From *Blackia, Petauristodon* differs in lesser amount of tooth crenulation, the proto- and metaconule, the "accessory loph," the secondary crests and the lack of a mesostylar crest of the paracone on the upper molars; the mesoconid, the well developed posterior cusps, the isolated mesostylid and the lack of an "anterosinuside" on the lower molars.

From *Pliopetaurista, Petauristodon* is different in the mesostyle, the "accessory loph" and the lack of a metaconule-spur on the upper molars; by the isolated mesostylid, the long mesoconid and the higher metaconid on the lower molars.

FAMILY EOMYIDAE DEPÉRET AND DOUXAMI, 1902

The eomyids are one of those rodent families whose history is known over a very long period. In North America representatives of this family are known from the Late Eocene until the Late Miocene, in Europe from the Lower Oligocene until the Pleistocene. It is curious that in this very long history no increase of size such as is known from a number of other rodent families can be observed. On the contrary, the youngest species of this family are to some extent even smaller than the oldest. Even more curious is that some forms do not undergo any morphological changes during this long history, at least as far as the dentition is concerned (unfortunately at present skull and skeleton of the eomyids are scarcely known). In the different epochs of this long history specialized forms were repeatedly developed, but they can be traced only over relatively short periods. And all indications suggest that these specialized forms often developed from the stock of those that remained primitive, hence independently of each other. These deviations from the primitive type (or specializations) almost all develop in one direction, to lophodonty, to some extent combined with a certain hypsodonty. As far as the dentition is concerned, these lophodont forms resemble each other astonishingly, although in some cases we are sure that they developed independently, thus in a parallel manner (for example, *Paradjidaumo, Pseudotheridomys,* and *Rhodanomys*).

In contrast to these specialized, lophodont forms, there are bunodont forms, doubtless correctly considered as primitive, because the earliest known representatives of the family—*Protadjidaumo* in America, *Eomys* in Europe—show teeth of this type. In addition, these bunodont forms look very much like the sciuravids, considered to be the ancestors of the eomyids. The relations between North American and European eomyids were recently studied by Fahlbusch in a very careful paper (1973). Therefore, I will limit my present study to those points on which I have a different opinion.

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[10] It seems possible to me that *P. jamesi* represents a synonym of *P. mathewsi.* Outside of a small difference in size the two species show hardly any differences. However, for a definite decision the material of *P. jamesi* is too fragmentary and partly too poorly preserved.

Pseudotheridomys

Historical Introduction

The genus *Pseudotheridomys* was established in 1926 by Schlosser for an eomyid from Haslach near Ulm, which he had described in 1884 as *Theridomys parvulus*. Fahlbusch (1969) described a second species, *P. pusillus*, of this genus. The form from Cournon called *P. schaubi* by Lavocat (1951) should, according to Fahlbush (1968:231), be regarded as a synonym of *P. parvulus*. Because of the great similarities of the dentition Wilson (1960) incorporated an eomyid from Quarry A (Martin Canyon, Colorado) in the genus *Pseudotheridomys*. Shotwell (1967*a*) described a new species *P. pagei*, from the Quartz Basin (Oregon).

Both Wilson (1960:72 and 74) and Black (1965:41) explained the dental similarities of forms from both sides of the Atlantic by a Burdigalian migration of *Pseudotheridomys* from Eurasia to North America. Fahlbusch (1973) concluded on the basis of an analysis of the evolutionary level of the oldest North American *Pseudotheridomys* (from Quarry A) that the immigration happened earlier, in the late Stampian or early "Aquitanian." All authors agree that the genus *Pseudotheridomys* immigrated to North America from Eurasia. As far as the chronological correspondence is concerned, there is no reason to object to this hypothesis. Following Fahlbusch's study (1970) of the changes of eomyid populations we can say with certainty that the genus *Pseudotheridomys* developed from the genus *Eomys* in the Late Oligocene of middle Europe, and the hitherto oldest North American *Pseudotheridomys*, *P. hesperus* from Quarry A, appears not before the Marslandian, thus later. To this it can be added that careful comparisons of the two American species with those from Europe do not furnish any fundamental morphological differences in the dentitions.

On the other hand, regarding the astonishing similarities that developed again and again within the whole family Eomyidae during this long history, the question arises if the resemblances of American and European forms could not have been developed independently from each other, in a parallel way. It is worth mentioning that all comparisons are necessarily confined to the dentition, because neither the skull nor the postcranial skeleton of these animals is known. In addition, just recently several examples of other groups have showed that dental features alone are often insufficient for recognizing phylogenetic relationships.

There is one argument for the hypothesis that those American and European eomyids now united within the genus *Pseudotheridomys* could have originated independently—now we can say with great certainty that lophodont eomyids developed from bunodont forms. These bunodont genera (*Protadjidaumo, Adjidaumo, Eomys, Leptodontomys*) are hardly distinguishable by the dentition (this is also obvious in Fahlbusch's new diagnosis for the genus *Eomys* [1970:104] which can be transferred easily to some members of the genus *Adjidaumo*). With good reasons Wilson (1960) pointed out that *Pseudotheridomys hesperus* shows no close relationship to any American eomyid. It has to be added to this observation that the history of the North American Eomyidae is very poorly documented after the Middle Oligocene and that new connecting forms would not be surprising. Comparing the European species of *Pseudotheridomys* with earlier eomyids, especially *Eomys*, the morphological relations are not immediately apparent. Not until the faunas of the fissure fillings from southern Germany—especially Gaimersheim—were known, were we informed that *Pseudotheridomys* developed from *Eomys*. The morphological changes which the dentition of *Pseudotheridomys* shows compared with that of *Eomys* are not numerous: (1) labiad elongation of the last syncline of the lower premolar and molars; (2) linguad elongation of the first syncline of the upper molars; (3) development of a first syncline on the upper premolar. As Plates 11 and 12 show, the North American *Pseudotheridomys* species correspond very well in these three features with the European. Thus there is not just one characteristic but a combination of three features in which *Pseudotheridomys* from the New World differs from other eomyids of the same continent, while sharing these features with some European forms. There are many reasons to believe that the compared North American and European forms of *Pseudotheridomys* are closely related. If other mammal groups did not show even more astonishing dental resemblance, which can be explained by convergence, I would consider the close relationship as proved. With an example of Eocene rodents I want to show how much derived forms, whose ancestors resemble each other, can correspond morphologically, without having any close phylogenetic relationship as proved. With an example of Eocene rodents I want to show how much derived forms, whose ancestors resemble each other, can correspond morphologically, without having any close phylogenetic relationship—certain Pseudosciuridae from Europe (*Protadelomys*, *Adelomys*; see Stehlin and Schaub, 1951:Figs. 26, 29, 311, 313) with their simple bunodont tooth pattern look very much like some bunodont Eomyidae. From these Pseudosciuridae there developed very probably lophodont forms of the *Theridomys* group (*Theridomys*, *Trechomys*, *Blainvillimys*; see Stehlin and Schaub, 1951:Figs. 29–33, 316–320), which in their form resemble very much the lophodont eomyids, especially *Pseudotheridomys*, that originated from bunodont ancestors.

In the Eomyidae there are more examples of certainly independent development of similar, more or less lophodont tooth patterns. In contrast to the above-mentioned example, in the following two cases the probably bunodont ancestral forms are not known: the lower dentition of *Centimanomys major* from the Chadronian of Colorado (Galbreath, 1955) shows great similarities to *Pseudotheridomys*, but is certainly not closely related to the latter. The conclusive feature for this similarity, in which *Centimanomys* is different from nearly all North American eomyids and which it has in common with *Pseudotheridomys*, is the fourth internal syncline of M_1 and M_2 extending far labially.

As a further example, *Meliakrouniomys* (Harris and Wood, 1969) from the Chadronian of Texas shows several features in common with the European genus *Ritteneria* (Stehlin and Schaub). The similarities of these two genera are based essentially on the complete interruption of the longitudinal ridge (Längsgrat) and the direct connection of the four main cusps by transverse lophs on the lower molars. As Emry (1972) demonstrated *Meliakrouniomys* is probably not an eomyid but a heteromyid, and thus a close phylogenetic relationship does not need to be discussed.

Comparing American and European representatives of the genus *Pseudotheridomys*, it is interesting that in the two continents different evolutionary trends are found. *Pseudotheridomys pagei* (Plates 11d and 12d) from the Barstovian of Oregon—the hitherto most recent *Pseudotheridomys*—is hardly distinguishable from *P. hesperus* (Plates 11e and 12e) of Quarry A; while in Europe, already in the Aquitanian, tendencies can be observed in *Pseudotheridomys*, which lead over to *Ligerimys*. Also the European genus *Keramidomys*, originating in the Middle Miocene, has to be regarded as a descendant of *Pseudotheridomys*. Thus we find the following situation: whereas *Pseudotheridomys* in North America does not continue differentiating, it splits in Europe into two lines in which the molar pattern is to some extent different from that of the ancestral genus.

In summary, the history of this genus, especially in North America, is insufficiently documented at present. If for the present no fundamental differences between North American and European species can be found, and therefore an intercontinental faunal exchange seems to be probable, I nevertheless consider it not impossible that the American and European forms developed independently from bunodont eomyids.

Leptodontomys

History of Investigation

The genus *Leptodontomys* was established by Shotwell (1956) on the basis of a single lower jaw fragment with incisor and premolar from the Hemphillian of Oregon. Later Shotwell (1967*a*) reported some isolated teeth from the Clarendonian of Oregon belonging to this genus (*Leptodontomys* sp.). Hugueney and Mein (1968) incorporated several Miocene and younger eomyids from different European localities in this genus (La Grive, Lissieu, Can Llobateres, Manchones, Schernfeld bei Eichstätt). In the meantime similar teeth were found also in Neudorf a.d. March, Franzensbad, Vieux Collonges, and Anwil. Finally Fahlbusch (1973) discussed exhaustively the relations of North American and European *Leptodontomys*. This author preferred the possibility of a Middle Miocene "migration" of *Leptodontomys* from Europe to North America to a derivation of the New World *Leptodontomys* from older American eomyids.

Morphological Particularities of Leptodontomys

As pointed out in the section on *Pseudotheridomys*, bunodont eomyids resemble each other very much in tooth pattern. Thus *Leptodontomys* differs from other bunodont forms, such as *Adjidaumo* and *Eomys*, only insignificantly. Among North American eomyids *Leptodontomys* is out of place in having a linguad anterior cingulum on the upper molars, otherwise a rather rare feature. The differences between *Leptodontomys* and *Adjidaumo* pointed out by Shotwell ("it [*Leptodontomys*] differs from this genus[*Adjidaumo*]by having a poorly-developed posterior cingulum, a smaller mesoconid, and widely separated protoconid and metaconid") all refer to the lower premolar and turned out to be largely invalid when more complete material from Black Butte was found. Also Fahlbusch (1973) and Hugueney and Mein (1968) attach great importance to the development of a linguad anterior cingulum on the upper molars.[11] The latter authors might have been led at least in part by this feature to unite American and European forms in the same genus (see emended diagnosis, Hugueney and Mein, 1968:200).

Discussion

Assignment of the European forms to *Leptodontomys* was suspicious to me from the beginning and after seeing Shotwell's original specimens from Oregon my doubts increased. We do not have any indications of the dispersal from one continent to the other. Supposition of a close relationship is based exclusively on the correspondence of the tooth pattern. Especially in cases like this, we must be very careful because the tooth pattern of *Leptodontomys* is certainly very primitive. This becomes apparent in comparing the tooth pattern of *Leptodontomys* with that of the earliest known eomyids such as *Protadjidaumo* and *Eomys*. So far as primitive forms are concerned, there is generally a risk to assume close phylogenetic relationships on the basis of morphological similarities to other primitive forms, where actually no relation exists. Comparing, for example, *Protadjidaumo* and *Leptodontomys* (see Plate 14b, e), it seems unlikely that the forms now united in the genus *Leptodontomys* represent in North America as well as in Europe different lines of eomyids that remained primitive.

Fahlbusch (1973) considers probable the extraction of *Leptodontomys* from the *Eomys rhodanicus* group. He assumes that *Leptodontomys* originated in Europe and immigrated to North America in the Middle Miocene. In my opinion there is nothing against tracing back the descent of *Leptodontomys* to the *Eomys rhodanicus* group, but for many reasons it seems to me more likely that the American *Leptodontomys* developed independently from the European. In *Protadjidaumo* (see Plate 14e) we have an American group to which, although separated by a long time interval, *Leptodontomys* can easily be traced morphologically. Among the Upper Eocene eomyid materials of the Badwater area (Wyoming) there is a form, possibly of the *Protadjidaumo* group, showing a well developed linguad anterior cingulum on the upper molars. That this cingulum is a primitive feature seems to be corroborated by the very old *Eomys* teeth from Hoogbuitsel clearly showing this feature too. Therefore, it seems to me more probable that the dental similarities of European and North American *Leptodontomys* may be explained in the following way: in the Early Tertiary the eomyids immigrated to Europe (see Discussion), after having almost certainly developed in North America from sciuravid ancestors. In both continents forms with a very primitive dentition similar to the common ancestor endured a long time (in America till the Upper Miocene, in Europe perhaps till the Early Pleistocene). Fahlbusch (1973) takes this possibility of two independent lines into consideration also but regards the possibility of a migration as more likely.

Morphological Differences between American and European Forms

A number of differences between forms of the two continents reinforced my opinion that in the case of *Leptodontomys* we are dealing with two largely independent lines, each of them confined to its continent. These are differences in the dentition but also in morphology of the lower jaw. I would not have attached more importance to the dental differences of the dentition than have other authors if I had not noticed that exactly those features differing North American and European *Leptodontomys* also separate the other eomyids of the two continents into two groups. Thus, the European *Leptodontomys* in these features links up closely with other eomyids from Europe, whereas the North American genus in these features corresponds with the eomyids of that continent. For example, the exterior synclines of the upper molars of most North American eomyids (especially of *Paradjidaumo* and *Adjidaumo*) reach less far lingually than those of European forms (most *Eomys* and especially *Ligerimys*; see Plate 13). Connected with this, the junction of the anteroloph with the protoloph in American forms lies generally in the middle of the tooth or somewhat labiad of it, whereas on upper molars from Europe this junction is located more lingually. In these features both *Leptodontomys* from Europe and those from America behave "continent-typically." The fourth interior syncline of the lower premolar and molars is a further feature apparently splitting the eomyids of both continents into two groups—so far as I have seen this syncline is little developed in American eomyids (for example, *Adjidaumo, Paradjidaumo, Aulolithomys, Namatomys, "Adjidaumo" quartzi*), but on the average distinctly better developed in European forms (Plate 14). In this feature *Leptodontomys* from North America are clearly different from those of Europe. In the development of these features the later European forms are possibly more primitive, because the oldest known eomyids, those from the Badwater Upper Eocene, show a similar development in part.

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[11] In this development of the linguad anterior cingulum *Leptodontomys* corresponds very well with the genus *Pseudadjidaumo*, introduced by Lindsay (1972). The differences between the two genera seem too vague, and I am of the opinion that *Pseudadjidaumo* is a synonym of *Leptodontomys*.

An essential difference between *Leptodontomys* from North America and Europe appears in the lower jaw. Outside of the dentition the lower jaw is for the moment the only element in which we can compare the *Leptodontomys* of the two continents. These differences, unlike those mentioned above, are not found in the other eomyid genera, but they do not seem to me to be less important systematically since the morphology of the lower jaw is otherwise very uniform in this family.

Differences of the Lower Jaw

For these comparisons the type of *L. oregonensis* from McKay Reservoir (Oregon) and two mandibles from La Grive were at my disposal (see Fig. 7). It is immediately apparent that the American jaw is more delicate than the European. Above all the section between the tip of the masseteric fossa and the upper margin of the horizontal ramus is distinctly higher in the specimens from La Grive. In addition the upper edge of the diastema is more curved in the La Grive jaws. Although the La Grive specimens have the upper edge of the anterior part of the diastema at the same level as that of the alveoli, the same edge on the type specimen from Oregon ranges somewhat lower (see projection Fig. 7). Behind M_3 the La Grive jaws show a distinct swelling caused by the end of the incisor. This swelling is lacking on the Oregon specimen. On the other hand the latter mandible shows a ledge extending from the base of the ascending ramus to the condyle which is lacking on the specimens from La Grive. In addition the lower margin of the jaws is curved in a different way: in the Oregon specimen the most distinct curvature is below M_3, in the specimens from La Grive, further back.

Possibly the most important difference between *Leptodontomys* from North America and Europe is found in the lower incisor. Although the type specimen from McKay Reservoir does not show the slightest trace of a crenulation, one appears distinctly on the incisor of *Leptodontomys* from La Grive (see Fig. 8 and Hugueney and Mein, 1968:196). Such enamel crenulations of the lower incisors are known from many eomyids (for example, *Eomys, Pseudotheridomys*) and are, in my opinion, important for systematics. In the case of *Leptodontomys* this feature alone seems to justify a generic separation for the European species previously referred to the genus.

Eomyops, new genus

Derivatio nominis.—Eomyops = Eomys-like.

Diagnosis.—Small eomyid with bunodont cheek teeth and crenulated lower incisor. Upper molars—with well developed linguad anterior cingulum; second and fourth exterior syncline mostly extending lingually past the middle of the tooth. Mesoloph short, somewhat anteriorly directed. On P_4, M_1, and M_2, fourth interior syncline well developed.

Type species.—Eomys catalaunicus Hartenberger, 1966, from Can Llobateres (Spain).

Included species.—Eomys catalaunicus Hartenberger, 1966; *Leptodontomys bodvanus* Janossy, 1972.

Stratigraphic and geographic range.—Middle Miocene (level of Neudorf a.d. March, NMU 6) to Lower Pleistocene (Schernfeld bei Eichstätt) of Europe, from Spain to Czechoslovakia.

Differential diagnosis.—From *Leptodontomys* Shotwell, 1956, *Eomyops* is different in—the distinct crenulation of the lower incisor, lacking on the incisor of *Leptodontomys*; the more robust and distinctly higher horizontal ramus of the mandible; in addition the mandible of *Eomyops* shows a swelling for the end of the incisor, lacking on the mandible of *Leptodontomys*; the better developed fourth interior syncline of the lower P, M_1, and M_2; the exterior synclines of the upper molars extending more lingually than on molars of *Leptodontomys*; the different course of the anterior branch of the proto-

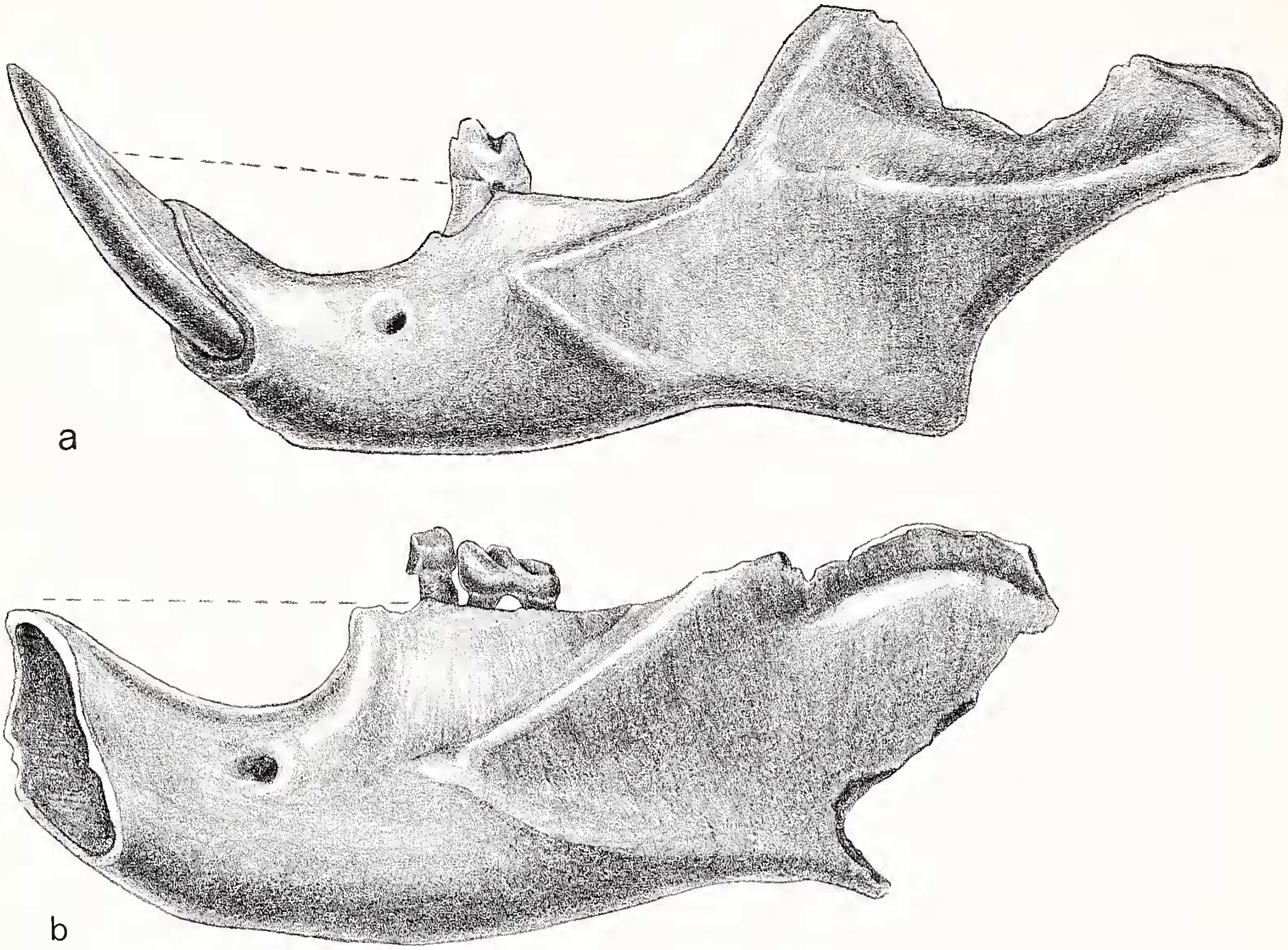

Fig. 7.—a) *Leptodontomys oregonensis* Shotwell, L mandible (invers) with I and P_4, (type) UO 3533, McKay Reservoir (Oregon), Hemphillian, 15×; b) *Eomyops* aff. *catalaunicus* (Hartenberger), L mandible (invers) with M_1 and M_2, La Grive (France), Middle Miocene, 15×.

conid and the metalophid, which in *Eomyops* extend more or less transversely and form a direct junction of proto- and metaconid, whereas in *Leptodontomys* these two lophs extend somewhat forward, joining only on the anterolophid or shortly before it.

From *Eomys* Schlosser, 1926, *Eomyops* is different in having a linguad anterior cingulum on the upper molars; exterior synclines of the upper molars extending more lingually; the short mesoloph of the upper molars, always anteriorly directed.

From *Adjidaumo* Hay, 1930, *Eomyops* is different in having a linguad anterior cingulum on the upper molars; the better developed fourth interior syncline on lower premolar and molars; the position of the foramen mentale, located distinctly higher in *Adjidaumo* (see Black, 1965:37, Fig. 6b).

As to *Pseudadjidaumo* Lindsay, 1972, see footnote 11.

Cotimus, Leidymys, Eumyarion, and *Eucricetodon*

(Family Cricetidae Stehlin and Schaub, 1951)

Historical Introduction

In his pioneer work on Tertiary cricetids, Schaub (1925) described a hamster from the Swiss molasse with the name "*Cricetodon helveticus*." He gave up the name "*Cricetodon medius*" (Lartet, 1851), established for a cricetid from Sansan, because no type was preserved and because it was impossible for him to identify "*C. medius*" among the three medium-sized cricetids from Sansan using the poor diagnosis of Lartet.[12] Fahlbusch (1964) split Schaub's genus *Cricetodon* and declared *C. helveticus* a synonym of *C. medius* Lartet, after having found a fragment of a maxillary from Sansan labeled with Lartet's own hand. In addition, he assigned *C. medius* to the American genus *Cotimus* Black, 1961. Shortly after doubts were heard about this assignment, probably essentially because only the type mandible of *Cotimus* was known (Freudenthal, 1965:297). Thaler (1966) expressed these doubts by introducing a new subgenus for the European species—*Eumyarion,* later established as a genus by Mein and Freudenthal (1971).

Two facts may contribute something to the solution of the *Cotimus* problem—first of all (personal communication, C. C. Black) the holotype of *Cotimus alicae* is not from the Upper Miocene (middle or late Barstovian) as initially stated, but from the Upper Miocene (middle or late Barstovian) as initially stated, but from the Lower Miocene (Arikareean). The type originates from a layer possibly representing an equivalent of the Gering Formation (personal communication, D. Rasmussen). In addition, Rasmussen found new materials of *Cotimus* at the type locality, among which there was an upper jaw. Judging from this jaw, *Cotimus* is without doubt a synonym of *Leidymys* (Wood, 1936). Even if these new discoveries shed new light on the discussion, the problem of the relations of North American and European forms is far from being solved. Hitherto lacking in the literature are extensive comparisons of species from both continents.

Comparisons of Leidymys *(*=Cotimus *Black) and* Eumyarion *(Thaler)*

In spite of the new materials from both continents the comparisons are basically still confined to dentitions.

Lower dentition.—On the basis of the lower incisor the two forms are easily distinguishable—*Leidymys* shows a distinctly flattened incisor anteriorly with a triangular cross section (see Plate 17e) and that of *Eumyarion* lacks the sharp exterior edge and is rather kidney-shaped in cross section. The thin enamel coating covers only the anterior surface of the incisor of *Leidymys* (as in *Eumys*), whereas on the incisor of *Eumyarion* the enamel seems to be thicker and extends from the anterior surface nearly to the middle of the lateral side of the tooth. The enamel stripes on the exterior face show differences (see Plate 17e)—the incisor of *Leidymys* shows three stripes of which two are close and somewhat lateral of the middle of the anterior face. The incisor of *Eumyarion,* on the other hand, shows only two, more separated, stripes. The molars of the two genera are very similar in size, but the lower incisor of *Eumyarion* is distinctly more slender compared with that of *Leidymys.*

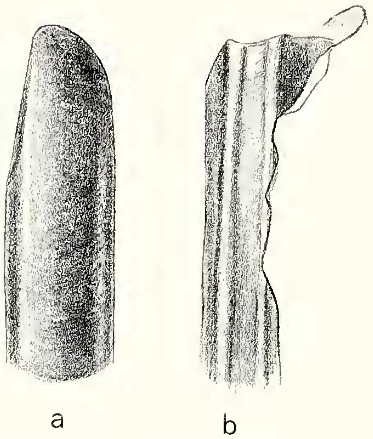

Fig. 8.—Comparison of the underside of the left lower incisor of a) *Leptodontomys oregonensis* Shotwell, UO 3633, McKay Reservoir (Oregon); b) *Eomyops* aff. *catalaunicus* (Hartenberger), NMBS, G.A. 635, La Grive (France). Both figures 25×.

Of the lower molars, M_1 shows the most distinct differences between the two forms—although the "Vorjochkante" (Schaub) in *Leidymys* always extends from the metaconid to the posterior branch of the protoconid (Schaub's "alte Vorjochkante"), it extends in *Eumyarion* from the metaconid to the anterior branch of the protoconid (Schaub's "neue Vorjochkante," Plate 16a and b). Connected with this the two anterior cusps of *Eumyarion* are more alternating than in *Leidymys,* with the metaconid more anteriorly located than the protoconid. The two anterior cusps of M_1 of *Leidymys* are less alternating. The great variation of connections of both anterior cusps and the anteroconid in all species of *Eumyarion* is very conspicuous (see Engesser, 1972:Figs. 109 and 111), whereas in *Leidymys* these connections show little variation.

In M_2 *Leidymys* is different from *Eumyarion* in sometimes having both the anterior "Vorjochkante" (the "new" one of Schaub) and the posterior (the "old") one. Such teeth show mostly a strong genuine mesostylid spur (see Plate 17d). The mesoconid is generally better developed in *Leidymys* than in *Eumyarion*. Also the metaconid of M_2 (as of M_3) of *Eumyarion* is joined more closely to the anterior cingulum than on M_2 of *Leidymys*.

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[12] According to Schaub (1925) at the Sansan locality besides *C. sansaniensis* and *C. minus,* four species of cricetids are present—*C. gaillardi, C. affinis, C. helveticus,* and *C. brevis.* As the extensive new materials from Sansan show, *C. affinis* is lacking at this locality.

The M_3 of *Eumyarion* and *Leidymys* are not very different, although that of *Eumyarion* is more reduced.

Schaub (1925) pointed out the importance of the middle spur of the lower molars as a criterion for determination of phylogenetic relationships—it must be determined whether it is a genuine mesostylid spur originating from the mesoconid or an elongated posterior branch of the protoconid ("Pseudomesostylidsporn" of Schaub). In this element *Leidymys* differs from *Eumyarion* only in those specimens showing a posterior branch of the protoconid extending to the metaconid. In this case a strong, genuine mesostylid spur is developed, often reaching to the lingual tooth margin (see M_1 of the holotype of *Leidymys alicae*, Plate 16b). In specimens showing a freely terminating posterior branch of the protoconid, thus having a "Pseudomesostylidsporn" (mostly in M_2 and M_3), there is in *Leidymys* as well as in *Eumyarion* no mesostylid spur present or only a very small one (see Plate 16a and b: *E. medius* and M_2 of the type of *L. alicae*).

Some M_1 and M_2 of *Leidymys* (*L. alicae* and *L. nematodon*) show a freely terminating posterior branch of the hypoconid in the fourth exterior syncline. This spur is only rarely found in *Eumyarion medius* from Sansan, but more frequently in the species *E. latior*, *E. bifidus*, and *E. leemanni*.

Upper dentition.—The upper molars of *Eumyarion* are more different from those of *Leidymys* than are the lower. Probably the most conspicuous and, for systematic relationships, the most important difference appears in the anterocone of M^1. In *Eumyarion* this anterocone is very wide, mostly somewhat bipartite (distinctly bipartite in *E. bifidus*) and its highest point is in the level of the exterior cusps (Plate 15a). The anterocone of M^1 of *Leidymys*, on the other hand, is distinctly narrower, always one-part and its highest point is between the top of the two anterior cusps (Plate 15b). In addition, the M^1 of *Eumyarion* in most species (*E. latior*, *medius* and *leemanni*) shows an anterior transverse spur ("vorderer Quersporn"), a feature which I did not observe in any tooth of *Leidymys* (Plate 17a–c). However, most specimens of *Leidymys* show a freely terminating anterior branch of the protoconid. This detail is found in *Eumyarion* too—in *E. bifidus* and, together with an anterior transverse spur, in *E. latior* (see Engesser, 1972: Fig. 106)—but never in *E. medius*. The connection of the mesostyle spur with the metacone (Plate 15a) is a peculiarity of *E. medius* and is found only rarely in other species.

In *Leidymys*, the "Vorjochkante" of M^2 leads directly to the protocone; in *Eumyarion*, on the other hand, it joins the posterior branch of the protocone. The M^2 of *Leidymys* (*L. alicae*, not *L. nematodon*) has a lingual anterior cingulum; one is lacking completely in *Eumyarion* (Plate 15a–c).

The M^3 of *Eumyarion* is more reduced than that of *Leidymys*. In *Eumyarion* the protocone covers almost the whole lingual face and the interior syncline is conspicuously shortened in favor of a central crater. In *Leidymys* the M^3 is, compared with M^2, only slightly reduced on its posterior end. It has a lingual anterior cingulum in *L. alicae* (see Plate 15b) and relatively well-developed metacone.

Lower jaw.—In the mandible, the only part of these animals other than the dentition that we can compare, differences between *Eumyarion* and *Leidymys* can be observed—the anterior part of the masseteric fossa, forming a short crista, in *Eumyarion* extends to below the anterior margin of M_1 or even farther anteriorly. As far as I observed in *Leidymys*, it extends only somewhat beyond the middle of M_1. On both lower jaws of *Leidymys* which I could compare (*L. alicae* and *L. nematodon*) there was a second, smaller foramen somewhat above and in front of the mental foramen. I never observed such a foramen in *Eumyarion*. The position of the mental foramen seems to be of little use for systematics, because the two mandibles of *Leidymys* having this detail showed different positions of it.

Discussion of the differences.—Most of these differences between *Leidymys* and *Eumyarion* do not seem to be basic, but rather represent different levels of similar developments. The "modern" features are without exception allotted to *Eumyarion* ("neue Vorjochkanten," reduced lingual anterior cingulum of M^2 and M^3, slightly developed mesoconid of the lower molars, reduced M^3, and others). *Leidymys alicae* is morphologically more primitive.

Comparison of Leidymys (=Cotimus) *and* Eucricetodon

Differences between *Eumyarion* and *Leidymys* seem to be due to different levels of development. However, *Leidymys* (=*Cotimus*) and *Eumyarion* are not here considered to be congeneric, as proposed by different authors. To establish the general differences between American and European forms it is necessary to compare *Leidymys* with a more or less contemporary cricetid such as *Eucricetodon collatus* (see Plates 15c and 16c). In *E. collatus* features are found again which showed *Leidymys* to be more primitive as compared with *Eumyarion*—"Alte Vorjochkanten" of M_1 and M_2, lingual anterior cingulum of M^2 and M^3, well-developed mesoconid on the lower molars. On the other hand, there are differences between *Leidymys* and *Eucricetodon* too—as in most Oligocene cricetids of Europe (exceptions, *Paracricetodon* and *Heterocricetodon*), *E. collatus* shows a distinctly more reduced M^3 than *Leidymys* (see Plate 15b and c). The anterocone of M^1 in many species of *Eucricetodon* (especially in *E. atavus* and *E. huerzeleri*) shows a tendency to become wider and to develop two peaks , not present in *Leidymys*. The lower incisor of *Eucricetodon* is distinctly more slender than that of *Leidymys* and its cross section is not triangular but rather drop-shaped (see Plate 17e). The enamel of the lower incisor of *Eucricetodon* extends more to the lateral face than in *Leidymys*. In addition, the incisor of *Eucricetodon* lacks the ledge on the lateral face, typical for *Leidymys* (and *Eumys*) and its enamel is thicker. In regard to these features of the incisor, *Eucricetodon* fits closer to *Eumyarion* than to *Leidymys*. The enamel stripes of the exterior face of the incisor seem less significant for these comparisons because they show a great variation in the different species of *Eucricetodon*. The same applies to the upper incisor showing, according to Wood (1937:257), stripes in *Leidymys lockingtonianus*. Certain species of *Eucricetodon* have striped upper incisors (for example, *E. collatus*), whereas others do not (for example, *E. huberi*).[13] In spite of these differences the dental similarities of *Eucricetodon* and *Leidymys* are striking. Vianey-Liaud (1972) raised the question whether *Eucricetodon* and *Leidymys* should be united in the same genus. Besides the differences mentioned above, I oppose such a union for other reasons. Certainly by Arikareean (or "Aquitanian") times, *Leidymys* as well as *Eucricetodon* had had a long separate evolution; *Leidymys* in North America being known since the Whitneyan (*L. vetus*), *Eucricetodon* in Europe since the lower Middle Oligocene (*E. atavus*). Wood (in Clark et al., 1964) traces the descent of *Leidymys* back to the *Eumys* group against which, in my opinion, there are no objections, because a form known as *L. vetus* seems to occupy an intermediate position between *Eumys* and *Leidymys*. The lower incisor of the latter with its nearly triangular cross section, the distinct exterior edge and the very thin enamel coat is very similar to that of *Eumys*. Both *Eumys* and *Leidymys* represent primitive forms, possibly resembling a common ancestor. This becomes evident by a comparison with *Simimys* from the Uintan (Upper Eocene), the earliest known cricetid (if it is really a cricetid!). Taking a look at Plates 15 and 16, it becomes obvious how widespread this tooth pattern is and over what a long time it held out, changing only in slight details. On these plates, forms are figured from the range between Orellan (Middle Oligocene) and Middle Miocene which are intended to point out how similar all these forms are, although coming from different continents and ages. As observed by other authors (among others, Schaub, 1925), some Recent cricetids of Madagascar show a similar tooth pattern. This resemblance easily could be dismissed as pure convergence, if the lower incisors did not show exactly the same two enamel stripes as, for example, *Eumyarion*!

In summary, *Eumyarion*, *Leidymys* (=*Cotimus*), *Eucricetodon*, and *Eumys* represent forms showing a very primitive tooth pattern and are therefore difficult to differentiate from each other on the basis of the dentition. The teeth may be throughout sufficient for differentiation of species and for determination of the evolutionary level, but for reconstruction of intercontinental relationships we need more complete remains.

DEMOCRICETODON AND *COPEMYS*

(Family Cricetidae)

History of Investigations

Fahlbusch (1964) divided the genus *Cricetodon* and united Schaub's species *brevis*, *affinis*, and *gaillardi* in the new genus *Democricetodon*. Influenced by the great dental similarity of *Democricetodon* and the American genus *Copemys* (Wood, 1936), Fahlbusch (1967) proposed that *Democricetodon* be regarded henceforth only as a subgenus of *Copemys*. This generic assignment did not meet with unanimous approval. In their new classification of the Tertiary cricetids from Europe, Mein and Freudenthal (1971) argued for a generic separation of *Copemys* and *Democricetodon*. This separation was substantiated above all by differences in the position and form of the incisive foramen. The same authors (1971:31–32) assigned *Democricetodon* to the subfamily Cricetinae (Murray, 1866), whereas they considered possible an affiliation of *Copemys* to the subfamily Hesperomyinae (Murray, 1866).

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[13] The value of such features of the incisor for the systematics is for the moment difficult to estimate. It is impossible to decide whether the incisor differences between these species indicate heterogeneity of the genus *Eucricetodon*, or whether these features vary even in closely related species and therefore are less useful for systematics. The heterogeneity of this group was pointed out by Thaler (1966:140) in introducing the new subgenus *Eucricetodon*.

Comparisons

Because the dentitions of *Copemys* and *Democricetodon* were already compared extensively by Fahlbusch (1967), I can confine my statement to a few details. The dentitions of some species of *Democricetodon* and *Copemys* resemble each other to such a degree that—as Lindsay (1972) wrote—even a specific distinction would be difficult, if they were found at the same locality. The only general difference between the forms of the two continents that I see can be observed on M^3—in all species of *Copemys* whose M^3 I know, this tooth is more reduced than in all species of *Democricetodon* (see Plate 18). This reduction affects not only the posterior half of the tooth, as is usual on M^3 of many other cricetids, but all elements except the protocone. Outside of this difference all details of the pattern typical for *Democricetodon* appear in the different species of *Copemys*—the short anteroconid of M_1, the anterior transverse spur of M^1, the spur in the exterior syncline of the lower molars.

Authors such as Fahlbusch (1967) and Lindsay (1972), arguing for a generic union of *Copemys* and *Democricetodon,* were apparently guided by the close similarities of the dentitions. But according to Mein and Freudenthal (1971:30)—and I agree in this respect with these authors—the dentition of the cricetids is perfectly useful for the distinction of different species, but not for the proof of phylogenetic relations above the species level. Mein and Freudenthal supported their opinion that the dental similarities of *Copemys* and *Democricetodon* have to be traced back to parallelism and that the two genera very probably belong to two different subfamilies (Hesperomyinae and Cricetinae), based on differences in the skull and skeleton. For the following reasons I do not agree in all points in this argument: these two authors attach great systematic importance to the position and shape of the incisive foramen. They state (1971:28) that *Democricetodon,* with its short incisive foramen with a posterior margin located anterior to the anterior end of M^1, is a representative of the Cricetinae. The incisive foramen of *Copemys,* on the other hand, continues between the upper molars as typical for the Hesperomyinae. The systematic value of this foramen seems to me somewhat doubtful, because in many cricetids it exhibits considerable variation—on certain skulls of *Eumys elegans* (AMNH collections) the posterior margin of this foramen occurs on the level of the anteroconid of M^1, but in many specimens assigned to the same species it is placed clearly more anteriorly (see Wood, 1937:Pl. 32). In the only skull of *Copemys* known to me in which the incisive foramen can be observed (Lindsay, 1972:Fig. 45), the foramen ends about at the level of the anterior margin of M^1. In *Peromyscus,* which developed almost certainly from *Copemys,* the posterior margin of this foramen is placed distinctly anterior to the anterior end of M^1. Mein and Freudenthal assign *Democricetodon* to the subfamily Cricetinae and give at the same time a provisional diagnosis of this subfamily based on the skeleton and skull. According to this diagnosis the mandible of *Democricetodon* is inclined lingually very distinctly, so that it is impossible to see the mental foramen in occlusal view. In addition, the humerus of *Democricetodon* shows an entepicondylar foramen. As to these two features, it can be said that the mandible of *Copemys* is actually less inclined lingually than that of *Democricetodon,* but also the humerus of *Copemys* shows an entepicondylar foramen (this knowledge I owe to Everett Lindsay, who kindly gave me a cast of a *Copemys* humerus).

For the moment it seems extreme to draw phylogenetic conclusions on the basis of these differences or similarities. According to Romer (1949) the entepicondylar foramen is a primitive feature and also occurs in other genera of cricetids (for example, *Fahlbuschia*).

Although questioning the value of the criteria mentioned by Mein and Freudenthal, for the following reasons I still hold that *Copemys* and *Democricetodon,* in spite of the similarities of the dentition, need not be closely related: as we can suppose for good reasons, probably all species of *Democricetodon* (as well as those of *Rotundomys* and *Kowalskia*) developed from a small and very primitive Lower Miocene form, which could have been closely connected with *Demoricetodon minor franconicus* from Erkertshofen (see Plates 18b and

19b).[14] Likewise it can be supposed that all North American species of *Copemys* descend from a primitive ancestral form, which might have been similar to *C. pagei* or *C. tenuis* (see Lindsay, 1972:77).

These most primitive known forms of both continents—*C. pagei* or *C. tenuis*, and *D. minor*—are very similar dentally (see Plates 18 and 19). This similarity led several authors to consider that both genera must be regarded as immigrants, descending from a common, probably Asiatic, ancestral form.

To me it is very strange that the evolved forms from North America and Europe, which can be derived with great probability from the primitive ones, look again very similar to each other. This similarity goes so far that, for example, *Copemys russelli* or *C. barstowensis* show exactly the same details in the dentition as are typical for *Democricetodon gaillardi*—the long mesolophs or mesolophids, the anterior transverse spur of the exterior syncline of the lower molars, the start of a labial posterior cingulum of M_1 and M_2, and others (see Plates 18c and 19c). Even the bend of the "Vorjochkante" and the "Nachjochkante" of the lower molars, typical for *Democricetodon gaillardi*, can be observed in certain forms of *Copemys* (see Shotwell, 1967*b*:Fig. 6A). This certainly parallel evolution of the *Democricetodon* and *Copemys* groups continues in the Pliocene—on both sides of the Atlantic forms develop showing a bipartite division of the anterocone of M^1, a reduction of the posteriormost exterior syncline of the upper molars, and distinctly anteriorly directed "Jochkanten" of the lower molars (for example, *Peromyscus pliocaenicus* in North America, *Rotundomys* and *Kowalskia* in Europe). How can these similarities be explained?

1) Migration? The fact that we do not know direct ancestors either of *Copemys* or of *Democricetodon* is for many authors proof that both genera were "immigrants." This statement is extreme because there is no known representative from an earlier deposit than Barstovian. The statement that the morphological similarities of the evolved forms from both sides of the Atlantic were caused by another "immigration wave" does not seem very probable to me, because, as mentioned above, an origin from the more primitive forms on both sides of the Atlantic can be demonstrated with some degree of certainty.

2) Parallel evolution? However closely related *Democricetodon* and *Copemys* might be, whether—as Mein and Freudenthal believe—on the level of the subfamily at best, or—as Fahlbusch and Lindsay state—on the level of the genus, certain parallel developments, at least for the evolved forms, can hardly be denied. To seek the reason for these parallelisms in the same environmental conditions is not reasonable at present, because the functional significance and with it the selective value of these details of the tooth pattern are not understood.

3) Completely independent development? It is questionable whether *Copemys* could have developed completely independently of *Democricetodon*. Wood (*in* Clark et al., 1964) supposed *Copemys* to have arisen from the *Leidymys* group. However, *Copemys* was at that time much less completely known than at present and its generic union with *Democricetodon* had not yet been discussed. In any case, the possibility can not completely be excluded that both genera developed independently since the Oligocene, that *Copemys* consequently could have descended from *Leidymys* and *Democricetodon* from an Oligocene cricetid from Eurasia.

4) Common ancestral form? I incline toward the opinion that *Democricetodon* and *Copemys* descended from a common, probably Asiatic, ancestral form, and developed for some time in parallel. An interpretation of the similarities as pure convergence seems to me to be hardly possible. Even if we are not fully aware of the reasons leading to parallelisms, we should in no case underestimate the extent of similarities and morphological correspondences caused by such parallelisms. As far as systematic position is concerned, it is appropriate to leave *Democricetodon* and *Copemys* as two different genera. For the solution of this problem it is not so important in which geological stage the two lines converge, whether in the Upper Miocene or at an earlier level. Rather more important to me is the fact that starting from primitive forms there appeared evolutionary lines on both sides of the Atlantic, even if they enter upon the same ways. This fact justifies, in my opinion, a generic separation in

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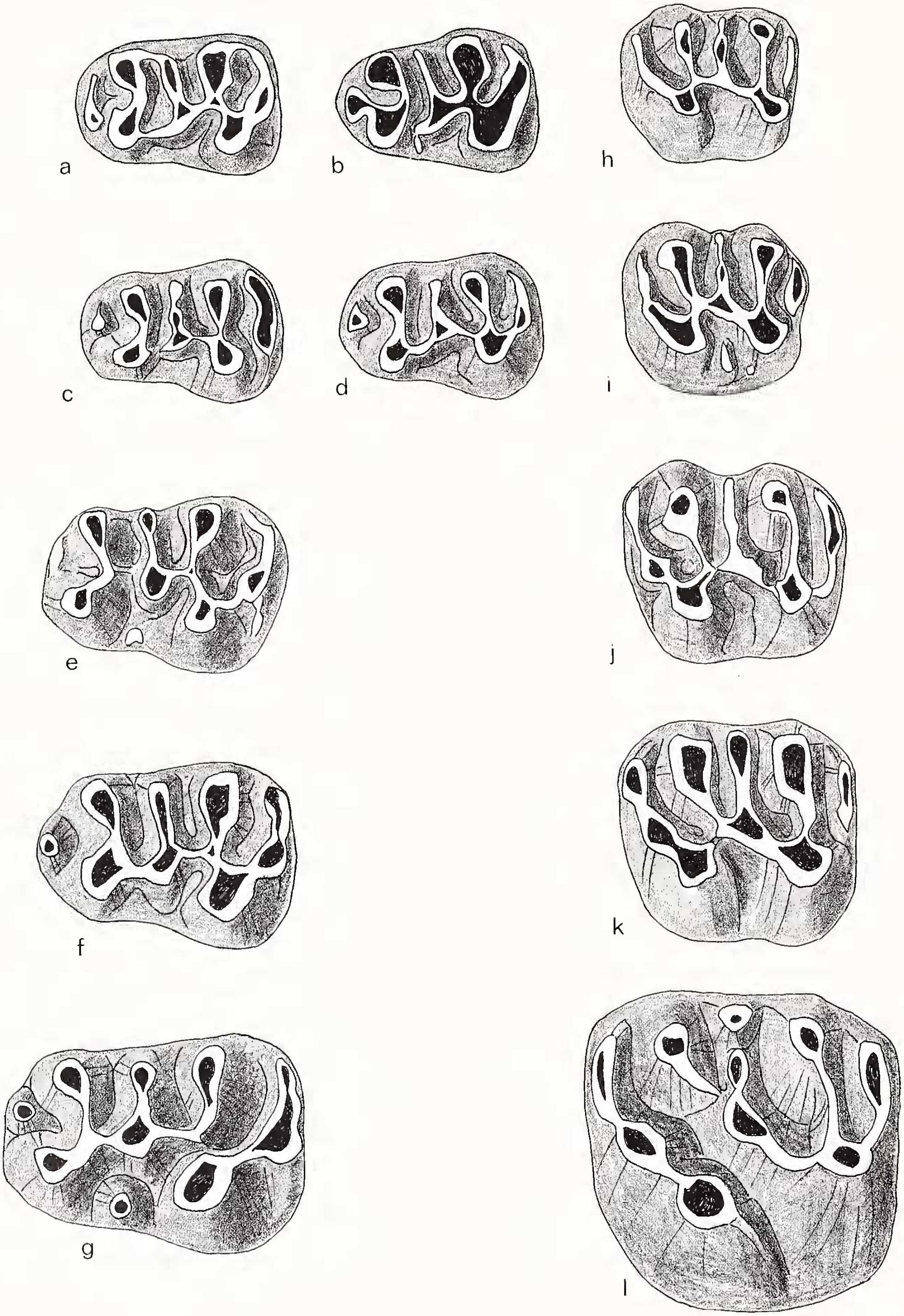
[14] According to Mein and Freudenthal (1971:28), *Democricetodon* from Villafeliche II A (NMU 4) and Erkertshofen (NMU 4) represent the oldest forms of the genus and they comply with all requirements which could be made for an ancestor of all later forms. The form of Villafeliche seems to me to comply better with these requirements because it shows an entoconid on M_3, in contrast to that from Erkertshofen (see Freudenthal, 1963:112). Nevertheless, I selected the form from Erkertshofen as an example for a primitive species (see Plate 18b and 19b), because no original material from Villafeliche was available to me.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cases like this one, where for the present the different forms can hardly be distinguished.

PLESIOSMINTHUS
(Family Zapodidae Coues, 1875)

History of Investigations

The genus *Plesiosminthus* was introduced by Viret (1926) for a form from St-Gérand-le-Puy (*P. schaubi*). Schaub, having recognized one year prior the affiliation to the Sicistinae of a tooth formerly identified as cricetid, described in his monograph (1930) on fossil Sicistinae two new species from the European Miocene and Oligocene (*P. myarion* from Chavroches and *P. promyarion* from Rickenbach). The first American sicistine was described as *Schaubeumys grangeri* by Wood (1935*a*), but this form was long regarded as a cricetid. Galbreath (1953) described a *Plesiosminthus*-like form from Quarry A (Martin Canyon, Colorado) but had some doubts about the generic assignment and called the form *Plesiosminthus*? *clivosus*. Black (1958) had the same doubts and proposed assigning *P.*? *clivosus* to the American genus *Schaubeumys* as he did the new species *S. sabrae* from the Miocene of Split Rock (Wyoming). Wilson (1960), describing the fourth American species (*S. galbreathi* from Quarry A), considered *Schaubeumys* as a subgenus of *Plesiosminthus*. He united the species *S. grangeri*, *sabrae*, and *galbreathi* in the subgenus *Schaubeumys*, whereas he incorporated the species *clivosus* together with the three European species in the subgenus *Plesiosminthus*. Likewise he considered the Mongolian genus *Parasminthus* Bohlin, 1946, as a subgenus of *Plesiosminthus*. Finally, Klingener (1966) described a form from the Valentine Formation of Nebraska (Upper Miocene) which he assigned to the genus ?*Plesiosminthus*, and introduced the giant form *Megasminthus tiheni*.

Comparisons of American and European Forms

The fact that several species of *Plesiosminthus* are known from each continent (three from Europe, four from America) makes it difficult to establish the common features of one group and to compare them with the characteristics of the group of the other continent. Larger sized teeth are common to all American forms, compared with the European. This is not surprising, since most American species are distinctly younger than the European. However, *Schaubeumys grangeri* from the lower Rosebud—the earliest American zapodid—is, according to the current stratigraphic correlations, the same age or even somewhat older than the middle "Aquitanian" *P. myarion* from Chavroches (NMU 2a) but still distinctly larger than this one.

As several authors have shown, the forms of both continents resemble one another morphologically. In spite of extensive comparisons, I found no general morphological differences, but only quantitative ones. Thus, on M_1 of European species the ridge extending anteriorly from the mesolophid almost always joins the protoconid, whereas in American forms this ridge extends straight anteriorly toward the anteroconid and contacts the ridge connecting protoconid and metaconid (see Fig. 9a–g). Only in the type jaw of *S. grangeri* does M_1 appear in this feature like the European forms (Fig. 9f). As an additional difference on M_1, the hypoconulid and mesoconid of American species generally seem to be better developed than in European. Likewise the protoconule of M^1 of American species seems to be more accentuated than in M^1 from Europe, where this cusp is often completely lacking (see Fig. 9h–l). On M^1 the "Vorjochkante" of many American specimens extends from the paracone to the mesoloph, whereas on all European specimens I compared, the "Vorjochkante"

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Fig. 9.—a–b) *Plesiosminthus myarion* Schaub, LM_1, NMBS, Chr. 761 and Chr. 759, Chavroches (France), Early Miocene (Aquitanian); c–d) *Plesiosminthus schaubi* Viret, LM_1, NMBS, Bst. 8838 and Bst. 8840, Coderet (France), Uppermost Oligocene; e) *Schaubeumys sabrae* Black, LM_1, CM 15854, Split Rock, Fremont Co., Wyoming, Hemingfordian; f) *Schaubeumys grangeri* Wood, LM_1, AMNH 13757 (invers), (type), Potato Creek, Pine Ridge, South Dakota, Lower Rosebud (Arikareean); g) *Megasminthus tiheni* Klingener, LM_1, CM 18855 (invers), Verdigre Quarry, Knox Co., Nebraska, Valentine Fm. (Late Miocene); h) *Plesiosminthus myarion* Schaub, LM^1, NMBS, Chr. 778 (invers), Chavroches (France), Early Miocene (Aquitanian); i) *Plesiosminthus schaubi* Viret, LM^1, NMBS, Bst. 690 (invers), Coderet (France), Uppermost Oligocene; j) *Schaubeumys sabrae* Black, LM^1, CM 15854 (invers), Split Rock, Fremont Co., Wyoming, Hemingfordian; k) *Schaubeumys grangeri* Wood, LM^1, AMNH 13757, Potato Creek, Pine Ridge, South Dakota, Lower Rosebud (Arikareean); l) *Megasminthus tiheni* Klingener, LM^1, CM 18864, Verdigre Quarry, Knox Co., Nebraska, Valentine Fm. (Late Miocene). All figures 25×.

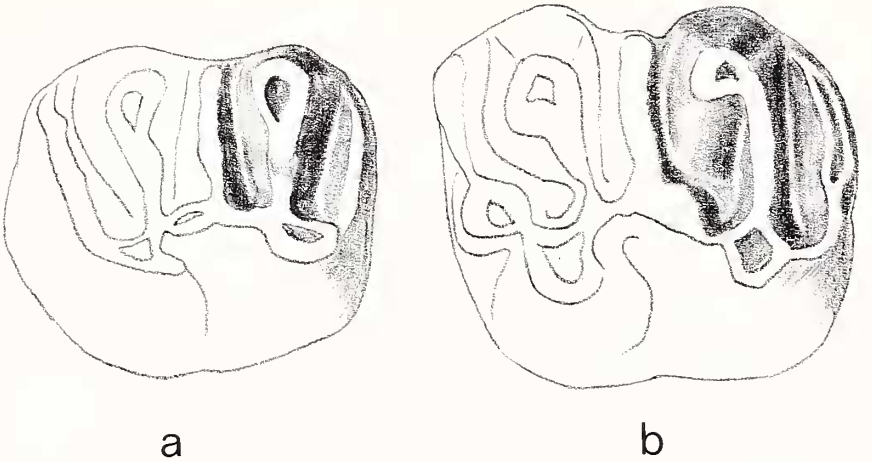

Fig. 10.—a) *Plesiosminthus myarion* Schaub, LM^1, NMBS, Sau. 3901, Saulcet (France), Early Miocene (Lower Aquitanian); b) *Schaubeumys sabrae* Black, LM^1, CM 15854, Split Rock, Fremont Co., Wyoming, Hemingfordian. Both figures 40×.

joined with the posterior branch of the protocone. There seems to be a difference in the metacone of M^1, and connected with this in the third exterior syncline—in American forms the metacone is a rotund cusp in occlusal view and on its lingual side the "Nachjochkante" sets on abruptly. This extends as a posteriorly bent, delicate ridge to the hypocone. The metacone of European forms is a rather elongated cusp, gradually passing into the hardly bent "Nachjochkante" (see Fig. 10). Finally, P^4 shows some differences—European species show only a wreath of little developed, small cusps, whereas in American species a relatively distinct anterior main cusp can be observed, surrounded by two or three side-cusps (see Plate 20a–b).

Even if none of the differences mentioned alone furnishes a criterion for distinguishing the groups of both continents, the total differences seem to be of some value for systematics. It is very interesting too that all mentioned features of the American forms appear again and in a higher degree in the dentition of the Late Miocene zapodid *Megasminthus tiheni* from the Nebraska Valentine Formation (see Fig. 9g and l). This fact suggests a close phylogenetic connection among American forms.

Discussion

As the above comparisons show, the American and European zapodids, united by many authors in the genus *Plesiosminthus*, are so similar to each other that—as Wilson (1960:86) pointed out—it is difficult to find constant differences. Once more the question arises how these similarities could originate. Wilson (1960:86) explained them by close phylogenetic relations, uniting the species of both continents in the same genus and stating that he was guided chiefly by two considerations—he found no distinct morphological differences to separate *P. clivosus*, *P. schaubi*, and *P. myarion*; secondly, *P. clivosus* is not the only mammal from Quarry A to show close relationship with European forms. As Wilson stated elsewhere (1960:21), the morphological similarities are more readily explained by "intermigration" than by parallelisms.

At what point of time did this "intermigration" take place? In a publication on the intercontinental correlations of the Miocene Wilson (1968) suggests for *Plesiosminthus* a "Burdigalian" immigration from Eurasia. This is an interesting interpretation considering that most American species first appear, according to the current correlations, somewhat after the latest European forms. Besides this the American forms are more advanced than the European. One fact, however, seems to contradict a "Burdigalian" immigration—the earliest American species, *S. grangeri*, is known from the lower Rosebud, which, according to most correlations, is pre-"Burdigalian." It seems possible that the *Plesiosminthus* group could have divided very early, perpaps in the Eocene or the Lower Oligocene and that the different lines did not develop in their dental morphology very far from the common ancestral form. It does not seem likely to me that these similarities between American and European *Plesiosminthus* are the result of pure convergence. The tooth pattern of this group is without any doubt a

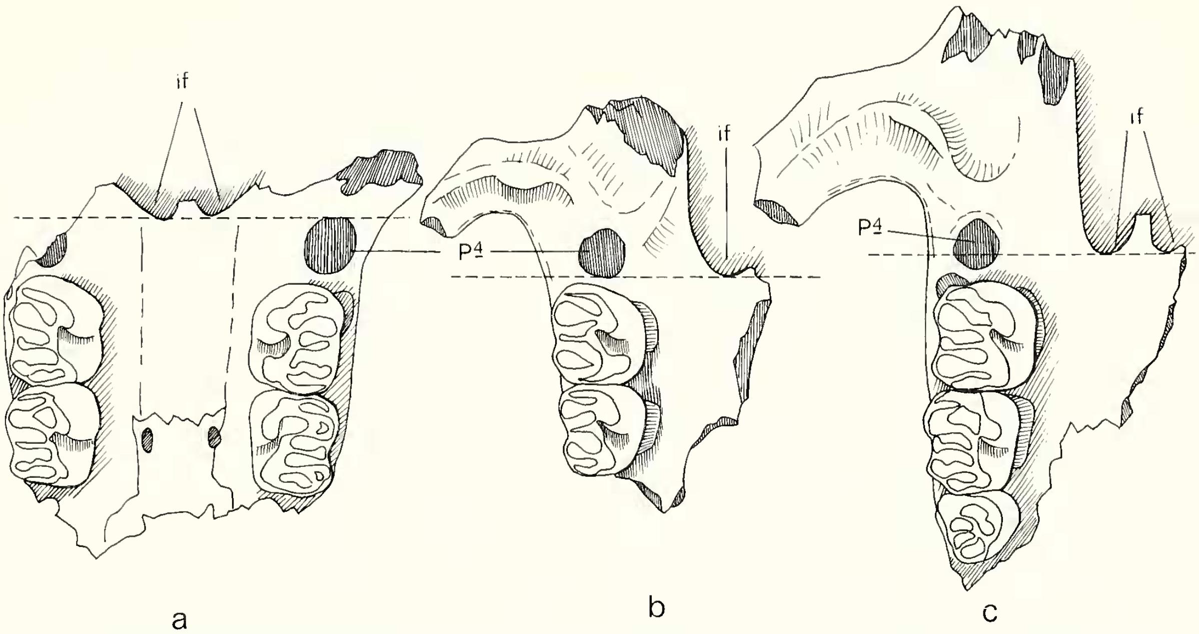

Fig. 11.—The position of the posterior edge of the incisive foramen with regard to the P^4. a) *Plesiosminthus myarion* Schaub, NMBS, Chr. 797, Chavroches (France); b) *Plesiosminthus schaubi* Viret, NMBS, Bst. 8856, Coderet (France); c) *Plesiosminthus myarion* Schaub, NMBS, Sau. 3899, Saulcet (France). if: posterior edge of the incisive foramen, P^4: alveolus of P^4. All figures 12×.

very primitive one, and even if parallelism were involved, similarity in these primitive forms (Wilson, 1949:23; Schaub, 1934:24) would indicate much more for the degree of relationship than in highly specialized forms, which in certain circumstances can reflect convergence from different evolutionary lines.

Simimys from the Sespe Eocene of California, whose systematic position is not yet clear, possibly could furnish an indication for early division of the zapodids. Even if *Simimys* cannot be considered as an ancestor of *Plesiosminthus* because of certain specializations, it still demonstrates that apparently in the Eocene in America forms existed that had a *Plesiosminthus*-like tooth pattern.

Another suggestion for an early division within the zapodids is furnished by *Parasminthus* from the Upper Oligocene of Mongolia (Bohlin, 1946), which besides many dental features common with the European *Plesiosminthus* shows some distinct differences.[15] The more or less contemporaneous occurrence of *Plesiosminthus* and *Parasminthus* indicates that at least in the Upper Oligocene of Eurasia two groups of forms existed.

As a final indication for early division within this group, the great variation undergone by the incisive foramen should be considered. Whereas in *Schaubeumys sabrae* (Black, 1958:Fig. 1A), *Parasminthus tangingoli* (Bohlin, 1946:Fig. 2/8), and *Plesiosminthus myarion* from Chavroches (see Fig. 11a), the posterior edge of this foramen is on the level of the anterior edge of P^4, in *S. clivosus* and *S. galbreathi* (Wilson, 1960:Figs. 126 and 128) it reaches the level of mid-P^4, and in *P. schaubi*, the level of the anterior edge of M^1 (see Fig. 11b). As far as the position of this foramen is concerned, there are distinct differences between the forms from Chavroches and from Saulcet, both assigned to the species *P. myarion* by Schaub—in the form from Saulcet the posterior edge of the foramen reaches the level of the middle or the posterior edge of P^4; in the Chavroches form the foramen ends distinctly anterior to P^4 (Fig. 12a and c).[16] Could it be possible that this variation indicates the existence of differ-

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[15] The most important difference between *Parasminthus* and *Plesiosminthus* seems to be the lack of a groove in the upper incisors of the former. Wood (1935*b*:225–226), who considered it possible that there is a single gene governing grooving or absence of grooving in heteromyid incisors, pointed out that the presence or absence of the groove is a systematic character of generic rank.

[16] At first sight it seems possible to explain the different positions of the posterior edge of the foramen incisivum in the forms from Branssat, Saulcet, and Chavroches as different phases in one advancing process. Because in such Recent zapodids as *Sicista* and *Zapus*, the foramen incisivum reaches farther back than in the Branssat form (that is, to the level of the protocone of M^1), this possibility becomes less probable.

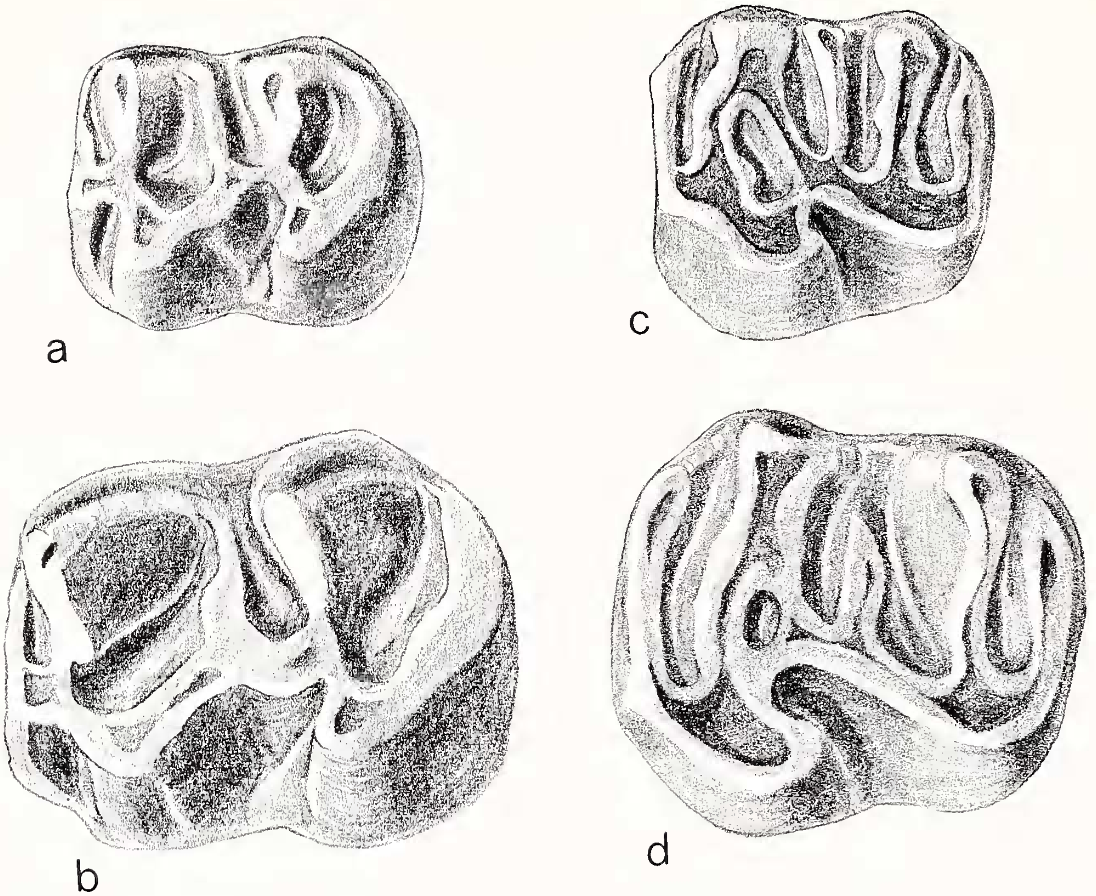


Fig. 12.—a) *Plesiosminthus myarion* Schaub, LM$_2$, NMBS, Sau. 3983, Saulcet (France), Early Miocene (Lower Aquitanian); b) *Eumyarion medius* (Lartet), LM$_2$, NMBS, Ss. 6721, Sansan (France), Middle Miocene; c) *Plesiosminthus myarion* Schaub, LM^2, NMBS, Sau. 3913, Saulcet (France), Early Miocene (Lower Aquitanian); d) *Eumyarion bifidus* (Fahlbusch), LM^2, BSPM 1952 XIV 89, Giggenhausen (Germany), Middle Miocene. All figures 40×.

ent lines, which are not distinguishable on the basis of the dental morphology?

The tooth type of *Plesiosminthus*, let us call it the "cricetoid" one, demonstrates for what long spaces of time such primitive tooth patterns can be maintained essentially unchanged and how slightly significant for systematics it is, as shown even in the Eocene with the dentition of *Simimys*, in the Oligocene with *Plesiosminthus*, certain cricetids and eomyids, and in the Upper Miocene, for example, in *Eumyarion*. Certain teeth of *Eumyarion* —especially M^2, M^3, M$_2$, and M$_3$—are barely distinguishable from corresponding teeth of *Plesiosminthus* (see Fig. 12, notice especially the double "Vorjochkante" of M^2 of both forms).

Summarizing, based on currently known specimens, correspondence of American and European *Plesiosminthus* can be explained as well as the result of an early zapodid division with little further morphological development as by a Burdigalian faunal exchange. Therefore and because of morphological differences, I propose to leave the American, Asiatic, and European species in the three separate genera, until we know more about the phylogenetic relations within this group.

DISCUSSION

In the preceding systematic section I tried to approach the problem of the relations between North American and European Miocene mammal faunas from a point of view different from that of most of my colleagues. At present there is much discussion of "migrations," which centers on the question of which groups passed from one continent to the other at what time and by which way. I have tried to show that outside of the "migration theory"—which actually is still a theory–there are other possible explanations for the often astonishing similarities of forms between the northern continents. Of course I am not the first to have envisaged other possibilities than "migration." Wilson (1960:21), for example, in discussing insectivores of Europe and North America, considered parallel evolution as a possibility besides "migration," although he did prefer the latter interpretation. Simpson (1947: 622, footnote) mentioned the possibility of convergence: "It is a conceivable alternative that some taxonomic groups are morphological but not phylogenetic and that they arose independently on the two continents. This has been claimed for many groups, but, if true at all, it must (in my opinion) be highly exceptional and can be ignored in an overall view."

I agree with Simpson that pure convergence, that is, development of a similar charcter in groups not closely related, is very unlikely, at least in the cases examined here. Nevertheless, this possibility cannot be excluded completely in forms with very poor records on both continents. Thus, in the case of the Miocene "sciuropterans" of California, it cannot be ruled out that these animals do not belong to the Sciuridae, and that we could be dealing with pure convergence. But in the other genera investigated it can hardly be contested that the forms were related at least at the family level.

Accordingly, the following alternatives remain to explain morphological similarity of forms from both continents:

1) the spread of similar forms to the other continent (="migration");

2) the spread of ancestors of similar looking forms from one continent to other, with

a) following parallel evolution over greater or lesser time periods, or

b) further development and conservation of certain primitive features over greater or lesser periods.

Common to all these alternatives is occurrence in each case of intercontinental dispersal. Differences between the alternatives concern only the point in phylogenetic history at which these spreads occurred.

My investigations of the genera treated in the systematic section suggest that possibilities 2a and 2b are more plausible than generally supposed.

Migration

The most popular current explanation for morphological similarities of forms from different continents is that of "migration." The use of the term "migration" implies probably that one understands the possibilities of a spread (what it is actually) much more extensively and also considers regions as passable, as long as they were more or less ice-free and relatively dry. However, using the term "migration" one has probably automatically in mind the migration of lemmings and birds of passage, that is, situations in which the animals are under a certain pressure and probably pass through areas not completely corresponding with their ecological needs.

In this connection it is much better to use the term "spread" which implies that the animals expand their range and open up new living space, and under normal conditions, they are subject to no pressure. (It can happen of course, that, for example by overpopulation, a certain pressure can arise, which can induce the animals to colonize areas not wholly suitable. However, such a pressure in my opinion would not persist as long as necessary, to overcome such enormous distances as in the present case.)

As to Neogene faunal exchange, I have some doubt with regard to the forms studied. Most current authors consider the Bering land bridge as an ideal spread route for land mammals (see Beringia History, 1973). There is evidence from several fields (paleobotany, malacology, sedimentology) that during the Tertiary there were repeated land connections across the Bering Strait. Investigations of large mammals especially suggest that this land bridge was utilized again and again (see H. Tobien, L. K. Gabunia, I. M. Novodvorskaya, N. M. Yanovskaya, and others, *in* Beringia History, 1973). Recent investigations show that during the Neogene certainly not a tropical or subtropical climate prevailed in the Bering area, but a best a temperate one. This is compatible with the view of S. F. Biske and Yu. P. Baranova (*in* Beringia History, 1973) that in the Oligocene and Miocene a change from a warm temperate to a cold temperate climate took place. In the Asian part of Beringia, a forest tundra appeared in the Middle Miocene and an alpine tundra was characteristic of the close of the Miocene. According to these and other investigations, essentially coinciding with each other, I see some difficulties for dwellers of tropical or subtropical forest areas, as many of the small mammal forms studied probably are, to colonize and pass through areas like Beringia. Simpson (1947) took into consideration the possibility that the spread of certain forms undergoes a delay by such climatic and ecologic barriers, that is, until a form adapted to the environment in question is developed. This is acceptable, but logically one should go beyond this, supposing that the "migrants" redeveloped a form adapted to the colonization of the warm areas in Middle Europe and North America. This seems very unlikely to me. With regard to the spread of tropical or subtropical animals, Simpson (1947:651) takes the view: "In any event, and contrary to what seems to be a widespread impression (e.g., J. W. Gregory, 1930), there is no evidence from the mammals that any truly tropical or subtropical animals ever migrated between Eurasia and North America and it is even dubious whether any specifically warm temperate groups made this journey." Thus we have to determine whether the forms studied here were actually dwellers of such warm climates. The ecologic and climatic ties of most of the 10 genera are not clear for the present. However, if conclusions from modern faunas are permissible, at least the fossil sciuropterans and *Lanthanotherium*, having Recent relatives mainly inhabiting tropical forest areas, may have lived under similar conditions. In addition we know that in the Miocene of Middle Europe there was a distinctly warmer climate than today and the same is applicable to the corresponding areas of North America (for example, the "Gray-beds" of Cuyama Valley in California, where four of the 10 genera are found). Very probably, *Lanthanotherium* and the sciuropterans were forest dwellers too, possibly also *Plesiosorex* and the Heterosoricinae, for their remains are mainly found together with typical forest faunas, and partly in lignites. In localities with typical steppe faunas, they are either very rare or are completely lacking. For such dwellers of warm forest biotopes the Bering area with its tundras certainly represented a virtually unsurmountable barrier, at least during the Neogene. However, this is not incompatible with inhabitants of temperate or cold climates having crossed the Bering area.

A further weak point in the theory of the Late Tertiary faunal exchange across Beringia is that this theory, at least as far as small mammals are concerned, is not strengthened by any evidence from eastern Asia. Certainly, there are well-documented Oligocene faunas known from the Hsanda Gol Formation in Mongolia (Matthew and Granger, 1923; Mellett, 1968) and from Taben-buluk in Kansu (Bohlin, 1942–1946). These faunas contain forms related to European and North American ones (for example, *Cricetops*, *Parasminthus*, *Eumys*, *Amphechinus*, Cylindrodontidae) but they do not furnish any indication of an intercontinental faunal exchange, for they are largely endemic. It may be argued that if migrations occurred, the migrants may have passed south or north of Mongolia. In my opinion, for climatic and ecological reasons the southern route may have been more advantageous for Oligocene and Miocene animals. If we want direct mammal paleontological evidence for such exchange, we have to look for Oligocene and Miocene mammals in southern Asia—in India, Burma, southern China, or perhaps in Indonesia. However, assuming such a southern distribution route, it becomes difficult to explain how the animals could pass over a land bridge situated so far north as the Bering bridge!

Doubts with respect to the Late Tertiary spread of mammals across Beringia are also based on the lack of fossil mammal remains in northern areas such as Siberia, Alaska, and northern Canada. As already mentioned, I cannot visualize such a spread as unidirectional, therefore, I suppose that animals able to pass over a land bridge as far north as the Bering bridge would have been living also in other northern areas.

No fewer problems arise assuming a post-Eocene faunal exchange over a northern Atlantic bridge. Because we have new evidence from continental drift, this theory has lost ground, although some authors still prefer the route across the northern Atlantic to that across the Bering Strait. Recently Strauch (1970) and Zhegallo (Beringia History, 1973) pleaded for the transatlantic route. In my opinion, this theory has the same handicaps as that of the spread over the Bering bridge—a northern Atlantic bridge would be equally situated very far north, and also from this area any fossil evidence is lacking. Furthermore, according to the newest paleomagnetic evidence, a direct land connection between Europe and North America after the Lower Eocene (from about 47 million years ago) is very doubtful.

The doubts advanced so far regarding intercontinental faunal exchange referred mainly to the climate and ecology of the distribution routes. I have also some doubts concerning the methods applied in mammal paleontology—the assumption of close relation of forms of both continents and the conclusions deduced from this that "migrations" have occurred are based above all on comparisons of dentitions. In my own investigations, several examples demonstrated that for determining phylogenetic relations, the dentition alone cannot be trusted absolutely. Of course, completely new problems arise here, because many fossil mammals are known by their dentition alone. As shown above, parallelism and the conservation of primitive features over a long period must considered. Therefore, the formerly generally used dictum—"What is not distinguishable morphologically is closely related"—must be questioned. This principle may be valid in cases in which we can compare more complete remains, such as skulls or skeletons, but has to be applied with extreme caution if we do not have anything but teeth to compare. As in the case of "*Cotimus*" close phylogenetic relations often have to be disproved when more complete remains become known. Therefore it is indispensable that in paleontology of mammals, and especially of small mammals, we try to compare other structures besides the dentition.

Especially in earlier literature, the possibility of rafting was considered (Schlosser, 1911; recently also Lavocat, 1973). A typical example of this kind of spread was the recolonization of the volcanic island Krakatau. Rafting may be effective for crossing of an arm of the sea or from one island to another. For the spread from one continent to another, this possibility can be dropped, in my opinion, because the chance that a single individual survives such a long transport is extremely small, not to mention the number of individuals necessary to build up a population.

PARALLEL EVOLUTION

To show parallel evolution conclusively is in most cases very difficult, and extensive fossil material should be available. But as many animals show, parallelism is not so rare and in many cases can produce astonishing correspondence of form. If morphological similarities can result from convergence in not-related forms, logically even more surprising similarities can be developed in related forms. As Wood (1947) stated convincingly, the chance of parallel evolution is greater in groups having specialized very early—for example, rodents or the Heterosoricinae—than in less specialized groups. With specialization, the spectrum of evolutionary possibilities is restricted, and the probability increases that the same development occurs two or more times.

Subsequent Adaptation and Trends

It is commonly assumed that identical or similar environmental conditions requiring a similar adaptation are important for the occurrence of parallelism. So, for example, the increasing hypsodonty in cricetids of the North American as well as of the European Upper Miocene and Pliocene, is probably connected with spread of the steppe environment in these areas. Such functional adaptations are not difficult to recognize as parallelism in most cases, for example, the jumping mouse type within the rodents (see Thenius, 1972:Fig. 3) or the fossorial type of rodents, insectivores, and marsupials.

When working on this paper, I was also faced with cases that I interpret as parallelism and in which the functional significance of a feature occurring in different groups cannot be understood easily. I found such strange phenomena in *Democricetodon* and *Copemys* and in *Plesiosorex*. One might ask again, are such parallelisms traceable to evolutionary trends? ("Trends" in the sense that the possibility for evolution in a certain direction can be hereditary.) I am aware of the danger of being branded as a partisan of an orthogenesis-theory. However, I do not intend to interpret any direction into the evolutionary process. I only want to consider the possibility of evolutionary trends to explain such cryptic parallelism in related groups, for the sake of discussion.

Conservation of Primitive Features

It is conspicuous that most of the small mammals from Europe and America studied here, which are usually placed in the same genus, have a primitive tooth pattern. In this category belong especially the bunodont eomyids, *Cotimus*, *Eumyarion*, the sciuropterans, *Lanthanotherium*, the Heterosoricinae, and *Plesiosorex*. In some of these cases the possibility of a "migration" cannot be completely excluded, but it seems more probable that the similarities between the pairs from the two continents result from conservation of certain primitive features. The group of *Eomys, Leptodontomys, Protadjidaumo,* and *Eomyops* in which the same tooth type was conserved from the Upper Eocene to the Pleistocene, or that of *Leidymys, Eumys,* and *Eumyarion,* in which the time range of this tooth pattern goes from the Middle Oligocene to the Upper Miocene, demonstrate over what long time periods a tooth pattern can be retained basically unchanged. In my opinion this possibility of long-range conservation of a tooth pattern is underestimated by colleagues, who consider as "immigrants" forms "suddenly" appearing in a layer without immediately earlier ancestral forms being known. This view overestimates very much the completeness of the available fossil record. As innumerable examples demonstrate, the fossil documentation of most mammal groups is incomplete. In addition, it should be considered that for animals that were rare in their lifetime or that lived in an area unsuitable for fossilization, there is scarcely a chance that their remains are ever found.

If one attempts to explain the similarities of Neogene mammals of North America and Europe as I did in the preceding part by parallel evolution or by conservation of primitive features, one also has to consider how the ancestors of these similar forms managed the trip from one continent to the other. Supposing an Early Tertiary faunal exchange some difficulties arise because according to present generally accepted opinion such an exchange across the Atlantic was not possible after the Early Eocene (McKenna, 1973). Because Europe and Asia were separated by the Turgai Straits marine barrier (McKenna, 1975) until the beginning of the Oligocene, and Eocene faunal exchange between North America and Europe via Asia was also hardly possible. However, it is conceivable that forms having reached Asia during the Eocene got to Europe after the disappearance of the Turgai barrier. Because we know very little at present about Tertiary faunas from Asia, it is also possible to suppose that some of the groups studied here had their center of evolution in Asia and spread from there to Europe and North America. There is nothing to object to an Early Tertiary spread across the Bering Strait because it can be considered certain that the Early Tertiary climate of the Bering area was much warmer than in the Neogene.

CONCLUSIONS

Investigation of 10 small mammal genera ostensibly occurring in North America as well as in Europe demonstrates that generic equivalence is very questionable, and that in three cases (*Limnoecus, Leptodontomys,* "*Cotimus*") is apparently incorrect, because important morphological differences between American and European forms can be found. In other cases these generic unions could not be disproved, but the insufficient documentation renders them dubious. Dental remains alone are often inadequate for illuminating phylogenetic relationships. Further, it becomes apparent that not all similarities between forms of both continents can be explained by "migrations" and that other possibilities, especially parallelism and conservatism, are more important than usually assumed.

LITERATURE CITED

Baudelot, S. 1972. Etude des Chiroptères, Insectivores et Rongeurs du Miocène de Sansan (Gers). Thèse Univ. Paul Sabatier Toulouse, 364 pp.

Beringia History. 1973. The Bering Land Bridge and its role for the history of Holarctic floras and faunas in the Late Cenozoic. Theses of the reports of All-Union Symposium. Acad. Sci. U.S.S.R. Khabarovsk.

Black, C. C. 1958. A new sicistine rodent from the Miocene of Wyoming. Breviora, 86:1–7.

———. 1961. Fossil mammals from Montana. Part 1. Additions to the Late Miocene Flint Creek local fauna. Ann. Carnegie Mus., 36:69–76.

———. 1965. Fossil mammals from Montana. Part 2. Rodents from the Early Oligocene Pipestone Springs local fauna. Ann. Carnegie Mus., 38:1–48.

Blainville, H. M. Ducrotay de. 1839–1864. Ostéographie des Mammifères. Tome 1, Livraison 6-H, Insectivores. Paris, 115 pp.

Bohlin, B. 1946. The fossil mammals from the Tertiary deposit of Tabenbuluk, western Kansu. Part II. Paleont. Sinica (new ser. C), 8b:1–259.

Butler, P. M. 1948. On the evolution of the skull and teeth in the Erinaceidae. Proc. Zool. Soc. London, 118:446–500.

———. 1969. Insectivores and bats from the Miocene of East Africa: new material. Pp. 1–37, *in* Fossil vertebrates of Africa (L. S. B. Leakey, ed.), Academic Press, New York and London, 1:ix + 1–102.

Clark, J. B., M. R. Dawson, and A. E. Wood. 1964. Fossil mammals from the Lower Pliocene of Fish Lake Valley, Nevada. Bull. Mus. Comp. Zool., Harvard Univ., 131:27–63.

Cope, E. D. 1873. Third notice of extinct vertebrata from the Tertiary of the plains. Paleont. Bull. (Philadelphia), 16:1–8.

Crochet, J. Y. 1968. Révision des Marsupiaux et des Insectivores des Phosphorites du Quercy. Thèse 3^{e} cycle, Fac. Sci. Paris, 119 pp. (not printed).

Crusafont, M., J. F. de Villalta, and J. Truyols. 1955. El Burdigalense continental de la cuenca del Vallés-Penedés. Diputacion provincial de Barcelona. Mem. Comun. Inst. Geologico, 12:1–272.

Dietrich, W. O. 1929. Referat über E. Stromers "Wirbeltiere im obermiocänen Flinz Münchens." Neues Jahrb. f. Mineral. etc. 1929, 3:776–778.

Doben-Florin, U. 1964. Die Spitzmäuse aus dem alt-Burdigalium von Wintershof-West bei Eichstätt in Bayern. Bayer. Akad. Wiss. Abh. Neue Folge, 117:1–82.

Emry, R. J. 1972. A new heteromyid rodent from the Early Oligocene of Natrona County, Wyoming. Proc. Biol. Soc. Washington, 85:179–190.

Engesser, B. 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). Tätigkeitsber. der naturf. Ges. Baselland, 28:37–363.

———. 1975. Revision der europäischen Heterosoricinae (Insectivora, Mammalia). Eclogae geol. Helv., 68:649–672.

Fahlbusch, V. 1964. Die Cricetiden (Mamm.) der Oberen Süsswasser-Molasse Bayerns. Akad. Wiss. Math.-nat. Kl. Abh. N.F., 118:1–134.

———. 1967. Die Beziehungen zwischen einigen Cricetiden (Mamm. Rodentia) des nordamerikanischen und europäischen Jungtertiärs. Palaeont. Z., 41:154–164.

———. 1968. Neue Eomyiden (Rodentia, Mamm.) aus einer aquitanen Spaltenfüllung von Wissenburg in Bayern. Mitt. Bayer. Staatssaml. Paläont. Hist. Geol., 8:219–245.

———. 1969. *Pseudotheridomys pusillus* n. sp. ein neuer Eomyide (Rodentia, Mamm.) aus dem Oligozän Süddeutschlands. N. Jb. Geol. Paläont. Mn., 1969:673–679.

———. 1970. Populationsverschiebungen bei tertiären Nagetieren, eine Studie an oligozänen und miozänen Eomyidae Europas. Abh. Bayer. Akad. Wiss. Math-naturwiss. Kl. N. F., 145:1–136.

———. 1973. Die stammesgeschichtlichen Beziehungen zwischen den Eomyiden (Mammalia, Rodentia) Nordamerikas und Europas. Mitt. Bayer. Staatssamml. Paläont. Hist. Geol., 11:141–175.

Filhol, H. 1884. Note sur une nouvelle espèce d'Insectivore du genre *Amphisorex*. Bull. Soc. Philomathique de Paris (7) 8, pp. 63–64.

———. 1888. Description de quelques mammifères nouveaux trouvés à Sansan. Bull. Soc. Philom. vol. 7.

Freudenthal, M. 1963. Entwicklungsstufen der miozänen Cricetodontinae (Mammalia, Rodentia) Mittelspaniens und ihre stratigraphische Bedeutung. Beaufortia, Zool. Mus. Amsterdam, 10:51–157.

———. 1965. Betrachtungen über die Gattung Cricetodon. Koninkl. Nederl. Akad. Wetensch. Amsterdam, Proc., Ser. B., 68:293–305.

Gaillard, C. 1915. Nouveau genre de musaraignes dans les dépôts miocènes de La Grive-Saint-Alban (Isère). Ann. Soc. Linnéenne de Lyon, 62:83–98.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of north-eastern Colorado. Univ. Kansas Paleont. Contrib., Vertebrata, 5:1–120.

———. 1955. A new eomyid rodent from the lower Oligocene of north-eastern Colorado. Trans. Kansas Acad. Sci., 58:75–78.

Gorgas, M. 1967. Vergleichend-anatomische Untersuchungen am Magen-Darm-Kanal der Sciuromorpha, Hystricomorpha und Caviomorpha (Rodentia). Z. Wiss. Zool., Leipzig, 175:237–404.

Gregory, J. W. 1930. The geological history of the Pacific Ocean. Geol. Soc. London, Quart. J., 86:72–136.

Hall, E. R. 1929. A second new genus of hedgehog from the Pliocene of Nevada. Univ. California Publ., Bull. Dept. Geol. Sci., 18:227–231.

Harris, J. M., and A. E. Wood. 1969. A new genus of eomyid rodent from the Oligocene Ash Springs local fauna of Trans-Pecos Texas. Pearce-Sellards Series, Texas Mem. Mus., 14:1–7.

Hartenberger, J.-L. 1966. Les rongeurs due Valesien (Miocène supérieur) de Can Llobateres (Sabadell, Espagne): Gliridae et Eomyidae. Bull. Soc. Géol. France (7), 8:596–604.

Hugueney, M., and P. Mein. 1968. Les Eomyides (Mammalia, Rodentia) néogènes de la région lyonnaise. Geobios, 1:187–203.

Hutchison, J. H. 1966. Notes on some upper Miocene shrews from Oregon. Bull. Oregon Univ. Mus. Nat. Hist., 2:1–23.

———. 1972. Review of the Insectivora from the early Miocene Sharps Formation of South Dakota. Contrib. Sci. Nat. Hist. Mus. Los Angeles, 235:1–16.

James, G. T. 1963. Paleontology and nonmarine Stratigraphy of the Cuyama Valley Badlands, California. Univ. California Publ., Geol. Sci., 45:1–154.

Klingener, D. 1966. Dipodoid Rodents from the Valentine Formation of Nebraska. Occ. Papers Mus. Zool. Univ. Michigan, 644:1–9.

Kretzoi, M. 1962. Fauna und Faunenhorizont von Csarnota. A. Magy. All. Foldt Intez. Evi Jelent. Budapest, pp. 344–382.

Lartet, E. 1851. Notice sur la colline de Sansan. Annuaire Dép. Gers. 1851 Auch. 47 pp.

Lavocat, R. 1951. Révision de la faune des mammifères oligocènes d'Auvergne et du Velay. Sciences et Avenir, Paris, 153 pp.

———. 1973. Les Rongeurs du Miocène d'Afrique orientale. Mem. Trav. Inst. Montpellier, 1:1–284.

Lindsay, E. H. 1972. Small mammal fossils from the Barstow Formation, California. Univ. California Publ. Geol. Sci., 93:1–104.

Macdonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., 125:139–238.

———. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Nat. Hist. Mus. Los Angeles Co. Mus., 8:1–82.

McDowell, S. B. 1958. The greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist., 115:117–214.

McGrew, P. 1941. The Aplodontoidea. Field Mus. Nat. Hist., Chicago, Geol. Ser., 9:1–30.

McKenna, M. C. 1973. Sweepstakes, Filters, Corridors, Noah's arks and beached Viking funeral ships in Paleogeography. Pp. 295–308, *in* Implications of continental drift to the earth sciences, Vol. 1 (D. H. Tarling and S. K. Runcorn, eds.), Academic Press, London and New York, 622 pp.

———. 1975. Fossil mammals and early Eocene North Atlantic land continuity. Ann. Missouri Bot. Garden, 62:335–353.

Matthew, W. D., and W. Granger. 1923. Nine new rodents from the Oligocene of Mongolia. Amer. Mus. Novit., 102:1–10.

Mawby, J. E. 1960. A new occurrence of *Heterosorex* Gaillard. J. Paleont., 34:950–956.

Major, F. 1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proc. Zool. Soc. London, pp. 179–215.

Mein, P. 1970. Les Sciuroptères (Mamm., Rod.) Néogènes d'Europe occidentale. Geobios, 3(3):1–53.

———. 1976. Biozonation du Néogène méditerranéen à partir des Mammifères. Proc. 6th Neogene Congr., Bratislava, September 1975.

Mein, P., and M. Freudenthal. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. Scripta Geologica, 2:1–37 (Leiden, 1971).

Mellett, J. S. 1968. The Oligocene Hsanda Gol Formation, Mongolia: a revised faunal list. Amer. Mus. Novit., 2318:1–16.

Palmowski, J., and H. Wachendorf. 1966. Eine unteroligozäne Wirbeltierfauna aus einer Spaltenfüllung in Herrlingen/Blau (Württ). Mitt. Bayer. Staatssamml. Paläont. Hist. Geol., 6:229–245.

Patterson, B., and P. O. McGrew. 1937. A soricid and two erinaceids from the White River Oligocene. Field Mus. Nat. Hist., Geol. Ser., 6:245–272.

Pomel, A. 1854. Catalogue méthodique et descriptif des vertébrés fossiles. Paris 1854.

Rensberger, J. M. 1975. *Haplomys* and its bearing on the origin of the Aplodontoid rodents. J. Mamm., 56:1–14.

Repenning, C. A. 1967. Subfamilies and genera of the Soricidae. Geol. Survey Prof. Paper, 565:1–74.

Romer, A. S. 1949. The vertebrate body. Saunders Co., Philadelphia and London, 643 pp.

Schaub, S. 1925. Die hamsterartigen Nagetiere des Tertiars und ihre lebenden Verwandten. Abh. Schweiz. Palaont. Ges., 45:3–112.

———. 1930. Fossile Sicistinae. Eclogae Geol. Helv., 23:616–637.

———. 1934. Ueber einige fossile Simplicidentaten aus China und der Mongolei. Abh. Schweiz. Paläont. Ges., 54:1–40.

Schlosser, M. 1884. Die Nager des europäischen Tertiärs nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. Palaeontographica, 31:1–143.

———. 1911. Beiträge zur Kenntnis der oligozänen Landsäugetiere aus dem Fayum: Aegypten. Beitr. Paläont. u. Geol. Oesterr.-Ung. u. des. Orients, 24:1–167.

———. 1926. Die Säugetierfauna von Peublanc (Dep. Allier). Soc. Sci. Nat. Croatica 38/39 (Kramberger-Festband), pp. 372–394.

Seemann, I. 1938. Die Insektenfresser, Fledermäuse und Nager aus der obermiozänen Braunkohle von Viehhausen bei Regensburg. Palaeontographica, 89, Abt. A., 55 pp.

Shotwell, J. A. 1956. Hemphilian mammalian assemblages from north-eastern Oregon. Bull. Geol. Soc. Amer., 67:717–738.

———. 1967*a*. Late Tertiary geomyoid rodents of Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 9:1–51.

———. 1967*b*. *Peromyscus* of the late Tertiary in Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 5:1–35.

———. 1968. Miocene mammals of southeast Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 14:1–67.

Simpson, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. America, 58:613–688.

Stehlin, H. G. 1940. Zur Stammesgeschichte der Soriciden. Eclogae Geol. Helv., 33:298–306.

Stehlin, H. G., and S. Schaub. 1951. Die Trigonodontie der simplicidentaten Nager. Schweiz. Palaeont. Abh., 67:1–385.

Stock, C. 1935. New genus of rodent from the Sespe Eocene. Bull. Geol. Soc. Amer., 46:61–68.

Strauch, F. 1970. Die Thule-Landbrücke als Wanderweg und Faunenscheide zwischen Atlantik und Skandik im Tertiär. Geol. Rundschau, 60(1): 381–417.

Stromer, E. 1940. Die jungtertiäre Fauna des Flinzes und des Schweiss-Sandes von München. Abh. Bayer. Akad. Wiss. math.-naturw. Abt. Neue Folge, 48:1–102.

Thaler, L. 1966. Les rongeurs fossiles du Bas-Languedoc. Mém. Mus. Nat. Hist. Nat. série C, Sc. de la Terre, 17:1–296.

Thenius, E. 1949. Zur Revision der Insektivoren des steirischen Tertiärs. Sitzungsber. Oesterr. Akad. Wiss., math.-naturw. Kl. Abt 1, 158. Bd. 9. u. 10. Heft. pp. 671–693.

———. 1969. Stammesgeschichte der Säugetiere (einschliesslich der Hominiden). Handb. Zool., Berlin, 8/2:1–722.

———. 1972. Grundzüge der Verbreitungsgeschichte der Säugetiere. Eine historische Tiergeographie. Gustav Fischer Stuttgart, 345 pp.

Trouessart, E.-L. 1909. *Neotracus sinensis*, a new insectivore of the Family Erinaceidae. Ann. Mag. Nat. Hist., serv. 8, 4:389–391.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. Bull. Amer. Mus. Nat. Hist. 135:217–284.

Vianey-Liaud, M. 1972. Contribution à l'étude des Cricétides oligocènes d'Europe occidentale. Palaeovertebrata, 5:1–43.

Villalta, J. F., and M. Crusafont. 1944. Nuevos insectivoros del Mioceno continental del Vallés-Panadés. Notas Commun. Inst. Geol. Min. España, 12:1–26.

Viret, J. 1926. Nouvelles observations relatives à la faune de Rongeurs de Saint-Gérand-le-Puy. C.-R. Acad. Sc., 183:71–72.

———. 1940. Etude sur quelques Erinacéidés fossiles (suite) genres *Plesiosorex, Lanthanotherium*. Trav. Lab. Geol. Fac. Sc. Lyon Fasc., 39(28):33–70.

———. 1946. Sur un nouvel exemplaire de *Plesiosorex* soricinoides Blainv. des argiles stampiennes de Marseille-St-André. Eclogae Geol. Helv., 39:314–317.

Viret, J., and H. Zapfe. 1951. Sur quelques Soricidés miocènes. Eclogae Geol. Helv., 44:411–426.

Webb, S. D. 1961. The first American record of *Lanthanotherium* Filhol. J. Paleont., 35:1085–1087.

Wilson, R. W. 1949. Additional Eocene rodent material from southern California. Carnegie Inst. Washington Publ., 584:1–25.

———. 1960. Early Miocene rodents and insectivores from Colorado. Univ. Kansas Paleont. Contrib., Vertebrata, 7:1–93.

———. 1968. Insectivores, rodents and intercontinental correlation of the Miocene. 23rd Int. Geol. Congr., 10:19–25.

Wood, A. E. 1935*a*. Two new genera of cricetid rodents from the Miocene of western United States. Amer. Mus. Novit., 789:1–3.

———. 1935*b*. Evolution and relationship of the heteromyid rodents. Ann. Carnegie Mus., 24:73–262.

———. 1936. The cricetid rodents described by Leidy and Cope from the Tertiary of North America. Amer. Mus. Novit., 822:1–8.

———. 1937. The mammalian fauna of the White River Oligocene. Part 2. Rodentia. Trans. Amer. Philos. Soc., new ser., 28:155–269.

———. 1947. Rodents—a study in evolution. Evolution, 1:154–162.

———. 1962. The early Tertiary rodents of the family Paramyidae. Trans. Amer. Philos. Soc., new ser., 53:1–261.

CAPTIONS FOR PLATES

Plate 1.—a) *Lanthanotherium sansaniense* Filhol; LM^1–M^3, M^1: NMBS, Ss. 846, M^2: NMBS, Ss. 862, M^3: NMBS, Ss. 6723; Sansan, France; Middle Miocene. b) *Lanthanotherium sawini* James; LM^1–M^3, M^1: UCMP 50122, M^2: UCMP 66779, M^3: UCMP 54600 (invers); loc. V-5847, Big Cat Quarry, Ventura Co., California (M^1 and M^2); loc. V-5656, Hedgehog locality (M^3); Early Clarendonian. c) *Lanthanotherium sanmiqueli* Villalta & Crusafont; LM^1–M^3, M^1: NMBS, C. L1. 25, M^2: NMBS, C. L1. 26 (invers); M^3: Coll. E. Heizmann, Stuttgart B 12; Can Llobateres, Spain; Late Miocene. d) *Hylomys suillus dorsalis* Thomas; LM^1–M^3, NMBS 8892; Northern Borneo; Recent. All figures 15×.

Plate 2.—a) *Lanthanotherium sansaniense* Filhol; LM$_1$–M$_3$, NMBS, Ss. 6727-29; Sansan, France; Middle Miocene. b) *Lanthanotherium sawini* James; LM$_2$–M$_3$ (invers) UCMP 54594; loc. V-5666, Kent Quarry, Cuyama Valley, California; Barstovian. c) *Ocajila makpiyahe* Macdonald; LM$_2$–M$_3$, SDSM 56105; loc. V-5360, Wounded Knee Area, South Dakota; Sharps Fm. (Early Arikareean). d) *Lanthanotherium sanmigueli* Villalta & Crusafont; LM$_1$–M$_3$, NMBS, C. L1. 28–30; Can Llobateres, Spain; Late Miocene. e) *Hylomys suillus dorsalis* Thomas; LM$_1$–M$_3$, NMBS 8892; Northern Borneo; Recent. All figures 15×.

Plate 3.—a) *Meterix* sp.; LP$_4$–M$_2$ (invers), UNSM 1410-47, Ft-40; Frontier, Nebraska; Kimball Fm. (Pliocene). b) *Plesiosorex coloradensis* Wilson; LP$_4$–M$_1$, KU 9989 (type); Quarry A, Martin Canyon, Colorado; Hemingfordian. c) *Plesiosorex schaffneri* Engesser; LP$_4$–M$_3$ (invers), NMBS, Al. 149 (type); Anwil, Switzerland; Middle Miocene. d) *Plesiosorex* cf. *soricinoides* (Blainville); LP$_3$–M$_3$, FSL 4428; Chaveroche, France; Early Miocene (Middle Aquitanian). All figures 15×.

Plate 4.—a) *Meterix* sp.; LP$_4$–M$_2$ (invers), UNSM 1410-47, Ft-40; Frontier, Nebraska; Kimball Fm. (Pliocene). b) *Plesiosorex coloradensis* Wilson; LP$_4$–M$_1$, KU 9989 (type) and LM$_2$ (invers) KU 10001; Quarry A, Martin Canyon, Colorado; Hemingfordian. c) *Plesiosorex schaffneri* Engesser; LM$_1$–M$_3$ (invers), NMBS, Al. 149 (type); Anwil, Switzerland; Middle Miocene. d) *Plesiosorex* cf. *soricinoides* (Blainville); LP$_3$–M$_3$, FSL 4428; Chaveroche, France; Early Miocene (Middle Aquitanian). All figures 15×.

Plate 5.—a) *Plesiosorex styriacus* (Hoffman); LM$_1$, NMBS, OSM 312 (invers); Rümikon, Canton of Zürich, Switzerland; Middle Miocene. b) *Plesiosorex* sp.; LM$_1$, BSPM, 1926 I 81 (invers); Grosslappen, Germany; Middle Miocene. c) *Plesiosorex schaffneri* Engesser; LM^1, NMBS, Al. 145 (invers); Anwil, Canton of Baselland, Switzerland; Middle Miocene. d) *Plesiosorex coloradensis* Wilson; LM^1, KU 9990 (invers); Quarry A, Martin Canyon, Colorado; Hemingfordian. e) *Meterix* sp.; LM^1, OU 22326 (invers); Ove, Quartz Basin, Oregon; Barstovian. All figures 15×.

Plate 6.—a) *Dinosorex sansaniensis* (Lartet); LP^4–M^3, NMBS, P^4: Ss. 901 (invers), M^1: Ss. 6687, M^2: Ss. 899, M^3: Ss. 6724; Sansan, France; Middle Miocene. b) *Pseudotrimylus roperi* (Wilson); LP^4–M^3, P^4: KU 10013, M^1–M^2: KU 10018, M^3: KU 10016; Quarry A, Martin Canyon, Colorado; Hemingfordian. c) *Domnina* sp.; LM^1–M^3 (invers), CM 10853; South of Reva Pass, Slim Buttes, Harding Co., South Dakota; Oligocene. All figures 20×.

Plate 7.—a) *Pseudotrimylus roperi* (Wilson); LM$_1$–M$_3$, KU 10020; Quarry A, Martin Canyon, Colorado; Hemingfordian. b) *Dinosorex zapfei* Engesser; LM$_1$–M$_3$, (type), NHW, 1975/1712/1; Neudorf a.d. March, CSSR; Middle Miocene. c) *Dinosorex huerzeleri* Engesser; LM$_1$–M$_3$, (type), MO, Rb. 101; Rickenbach, Canton Solothurn, Switzerland; Late Oligocene. d) *Pseudotrimylus* sp.; LM$_1$–M$_2$, CM 10922; Lawson Ranch, Goshen Co., Wyoming; Lower Orellan(?). e) *Domnina* sp.; LM$_1$–M$_3$, CM 10403; Pipestone Springs, Jefferson Co., Montana; Chadronian. f) *Quercysorex primaevus* (Filhol); LM$_1$–M$_2$ (invers), (type), MHNP, Qu. 8681; Lamandine (Quercy); Middle Oligocene(?). All figures 20×.

Plate 8.—a) *Dinosorex sansaniensis* (Lartet); L mandible with I, M$_1$ –M$_3$, NMBS, Ss. 603; Sansan, France; Middle Miocene. b) *Pseudotrimylus roperi* (Wilson); L mandible with I, M$_1$–M$_2$, KU 10030; Quarry A, Martin Canyon, Colorado; Hemingfordian. c) *Pseudotrimylus roperi* (Wilson); L mandible with M$_1$–M$_3$, KU 10020; Quarry A, Martin Canyon, Colorado; Hemingfordian. All figures 8×.

Plate 9.—a) *Petauristodon mathewsi* (James); LM^1–M^2, UCMP 55514; loc. 5847, Cuyama Valley, California; Early Clarendonian. b) *Prosciurus* sp.; LP^3–M^2, CM 9316; North of Pipestone Springs, Montana; Chadronian. c) *Forsythia gaudryi* (Gaillard); LM$^{1/2}$, FSL 65433; La Grive, France; Middle Miocene; LM$^{1/2}$, NMBS, Al. 225; Anwil, Switzerland; Middle Miocene. d) *Miopetaurista albanensis* (Major); LP^3–M^1, NMBS, Al. 215–217; Anwil, Switzerland; Middle Miocene. All figures 15×.

Plate 10.—a) *Petauristodon mathewsi* (James); LP$_4$–M$_2$ (invers), UCMP 54516; loc. V-5662 Cuyama Valley, California; Late Clarendonian. b) *Prosciurus* sp.; LP$_4$–M$_3$, CM 9321; Pipestone Springs, north of tracks, Montana; Chadronian. c) *Forsythia gaudryi* (Gaillard); LM$_1$ and M$_3$, Al. 222 and Al. 223, NMBS; Anwil, BL, Switzerland; Middle Miocene. d) *Plesiospermophilus angustidens* Filhol; LP$_4$–M$_3$, Q. U. 273, NMBS; Quercy, France; Oligocene. All figures 15×.

Plate 11.—a) *Pseudotheridomys* sp.; LP^4–M^3, NMBS, P^4: G.B. 251, M^1: G.B. 266, M^2: G.B. 272 (invers), M^3: G.B. 278; Estrepouy, France; Early Miocene. b) *Pseudotheridomys parvulus* Schlosser; LP^4–M^3, NMBS, P^4: C.G. 646, M^1: C.G. 849, M^2: C.G. 850, M^3: C.G. 838; Laugnac, France; Early Miocene. c) *Pseudotheridomys* aff. *parvulus* Schlosser; LP^4–M^3, NMBS, P^4: Sau. 4271, M^1–M^2: Sau. 3703, M^3: Sau. 4162: Saulcet, France; Early Miocene. d) *Pseudotheridomys pagei* Shotwell; LP^4–M^3, P^4: UO 22720, M^1: UO 22710, M^2–M^3: UO 24414; Quartz Basin, Oregon; Barstovian. e) *Pseudotheridomys hesperus* Wilson; LP^4–M^1, KU 10200 (invers) and KU 10201 (invers); Quarry A, Martin Canyon, Colorado; Hemingfordian. All figures 30×.

Plate 12.—a) *Pseudotheridomys* sp.; LP$_4$–M$_3$, NMBS, P$_4$: G.B. 221, M$_1$: G.B. 228, M$_2$: G.B. 234, M$_3$: G.B. 233; Estrepouy, France; Early Miocene. b) *Pseudotheridomys parvulus* Schlosser; LP$_4$–M$_3$, NMBS, P$_4$–M$_2$: C.G. 436, M$_3$: C.G. 861; Laugnac, France; Early Miocene. c) *Pseudotheridomys* aff. *parvulus* Schlosser; LP$_4$–M$_3$, NMBS, P$_4$–M$_2$: Sau. 4974, M$_3$: Sau. 4170 (invers); Saulcet, France; Early Miocene. d) *Pseudotheridomys pagei* Shotwell; LP$_4$–M$_2$, U.O. 22708; Quartz Basin, Oregon U.O. loc. 2465; Barstovian. e) *Pseudotheridomys hesperus* Wilson; LP$_4$–M$_2$, KU 10195 (type); Quarry A, Martin Canyon, Colorado; Hemingfordian. All figures 30×.

Plate 13.—a) *Eomyops catalaunicus* (Hartenberger); LP^4–M^2, NMBS, P^4: C. Ll. 1, M^1: C. Ll. 3 (invers), M^2: C. Ll. 2; Can Llobateres, Spain; Late Miocene. b) *Leptodontomys* sp.; LP^4–M^2, P^4: U.O. 24852, M^1: U.O. 24849, M^2: U.O. 25285; Black Butte, Oregon; Clarendonian. c) *Eomys zitteli* Schlosser; LP^4–M^2, P^4: CM 24100, M^1: CM 24101, M^2: CM 24099; Gaimersheim, Germany; Late Oligocene. d) *Adjidaumo minimus* (Matthew); LP^4–M^2 (invers), NMNH 186671; South Fork of Lone Tree Gulch, Natrona Co., Wyoming; Early Oligocene. e) ?*Protadjidaumo typus* Burke; LM$^{1/2}$ (invers), CM 9955; Lapoint, West of Vernal, Utah; Duchesne River Fm.; Late Eocene. All figures 30×.

Plate 14.—a) *Eomyops catalaunicus* (Hartenberger); LP$_4$–M$_3$, NMBS, P$_4$: C. Ll. 4, M$_1$: C. Ll. 5 (invers), M$_2$: C. Ll. 6, M$_3$: C. Ll. 7 (invers); Can Llobateres, Spain; Late Miocene. b) P$_4$: *Leptodontomys oregonensis* Shotwell; UO 3633 (invers), type, McKay Reservoir, Oregon; Hemphillian. M$_1$–M$_3$: *Leptodontomys* sp.; M$_1$: UO 25283, M$_2$: UO 25278, M$_3$: UO 25274 (invers); UO loc. 2500, Black Butte, Oregon; Clarendonian. c) *Eomys zitteli* Schlosser; LP$_4$–M$_3$, CM 24094; Gaimersheim, Germany; Late Oligocene. d) *Adjidaumo minimus* (Matthew); LP$_4$–M$_2$ (invers), CM 9213; Pipestone Springs, Montana; Chadronian. e) *Protadjidaumo typus* Burke; LP$_4$–M$_2$, CM 11931; Lapoint, West of Vernal, Utah; Duchesne River Fm., Late Eocene. All figures 30×.

Plate 15.—a) *Eumyarion medius* (Lartet); LM$_1$–M$_3$ (invers), NMBS, Ss. 665; Sansan, France; Middle Miocene. b) *Leidymys* (=*Cotimus*) *alicae* (Black); LM$_1$–M$_3$ (invers), KU 18395; Cabbage Patch, Montana; Early Arikareean. c) *Eucricetodon collatus* (Schaub); LM$_1$–M$_3$, NMBS, Bd. 40; Boudry II, NE, Switzerland; Early Aquitanian. All figures 30×.

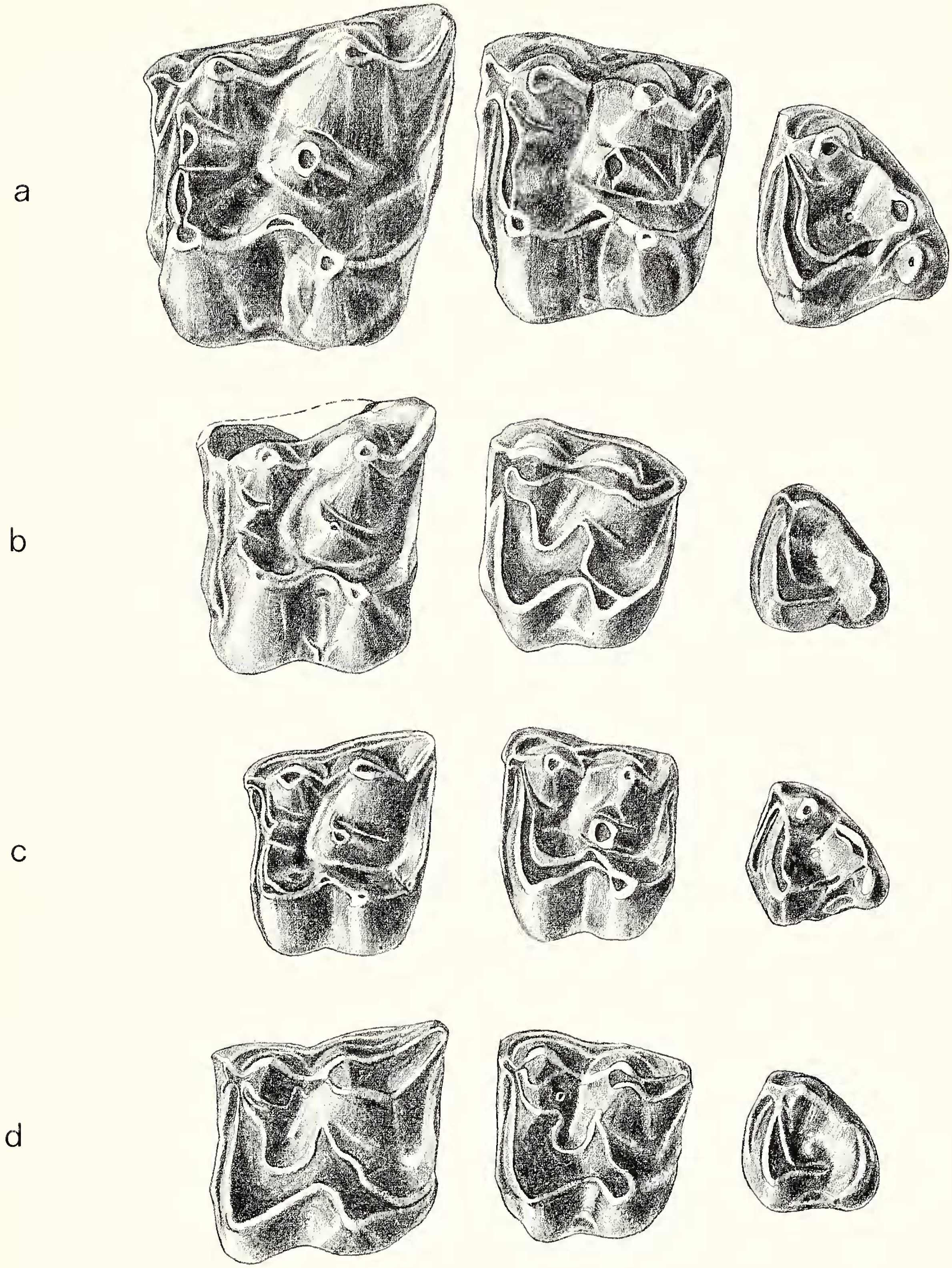
Plate 16.—a) *Eumyarion medius* (Lartet); LM_1–M_3, NMBS, Ss. 669; Sansan, France; Middle Miocene. b) *Leidymys* (*=Cotimus*) *alicae* (Black); LM_1–M_3, (type), CM 8868; Flint Creek, Montana; Early Arikareean. c) *Eucricetodon collatus* (Schaub); LM_1–M_3, NMBS, Pa. 13196; Paulhiac, France; Early Aquitanian. d) *Eumys* sp.; LM_1–M_3, CM 9711; Warbonnet Creek, Sioux Co., Nebraska; Oreodon Beds (Orellan). All figures 30×.

Plate 17.—a) *Leidymys* sp.; LM^1, KU 1808; Cabbage Patch, Montana; Middle Arikareean; 30×. b) *Leidymys alicae* (Black); LM^1, KU, without number; Cabbage Patch, Montana, horizon 58-2; Early Arikareean; 30×. c) *Eumyarion medius* (Lartet); LM^1, NMBS, Ss. 6722; Sansan, France; Middle Miocene. d) *Leidymys* sp.; LM_2 (invers), KU 1833; Cabbage Patch, Montana, horizon MV 6504 SQ; Middle Arikareean; 30×. e) Underside of left lower incisors of (1) *Leidymys alicae* (Black) KU 18394 Cabbage Patch, Montana; (2) *Eumyarion medius* (Lartet), NMBS, Ss. 669; Sansan, France; (3) *Eucricetodon collatus* (Schaub) NMBS, Cod. 188 Coderet, France; 15×.

Plate 18.—a) *Democricetodon gaillardi* (Schaub); LM^1–M^3 (invers), NMBS, Ss. 676; Sansan, France; Middle Miocene. b) *Democricetodon minor franconicus* Fahlbusch; LM^1–M^2, NMBS, Erk. 7-8; Erkertshofen, Germany; Lower Miocene. c) *Copemys russelli* (James); LM^1–M^3 (invers), UCMP 55507; loc. V-5847, Big Cat Quarry, Cuyama Valley, California; Early Clarendonian. d) *Copemys tenuis* Lindsay; LM^1, UCMP 75367; loc. V-65134, Barstow Fm., Southern California; Barstovian. All figures 30×.

Plate 19.—a) *Democricetodon gaillardi* (Schaub); LM_1–M_3, NMBS, M_1–M_2: Ss. 682, M_3: Ss. 6730; Sansan, France; Middle Miocene. b) *Democricetodon minor franconicus* Fahlbusch; LM_1–M_3, NMBS, Erk. 4-6; Erkertshofen, Germany; Lower Miocene. c) *Copemys barstowensis* Lindsay; LM_1–M_2, M_1: UCMP 74415, M_2: UCMP 74457; loc. V-5501 and V-5253 Barstow Fm., California; Barstovian. d) *Copemys tenuis* Lindsay; LM_1, UCMP 74511; loc. V-65150 Barstow Fm., California; Barstovian. All figures 30×.

Plate 20.—a) *Schaubeumys sabrae* Black; LP^4–M^2, CM 13529; Split Rock, Fremont Co., Wyoming; Hemingfordian. b) *Plesiosminthus schaubi* Viret; LP^4–M^2, NMBS, Bst. 8832; Coderet, France; Uppermost Oligocene. c) *Schaubeumys sabrae* Black; LM_1–M_2, CM 14774; Split Rock, Fremont Co., Wyoming; Hemingfordian. d) *Plesiosminthus schaubi* Viret; LM_1–M_2, NMBS, Bst. 8837; Coderet, France; Uppermost Oligocene. All figures 40×.



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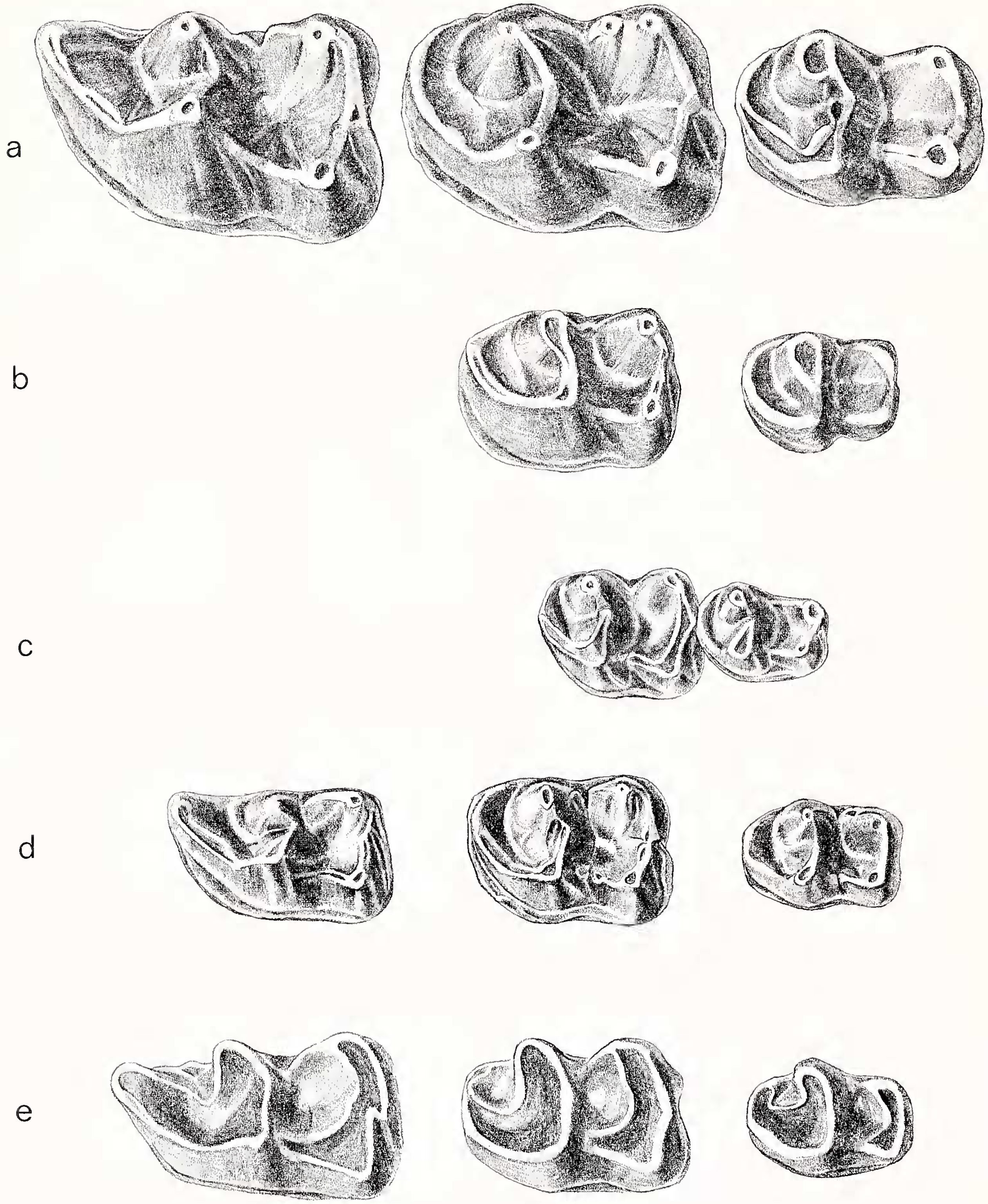

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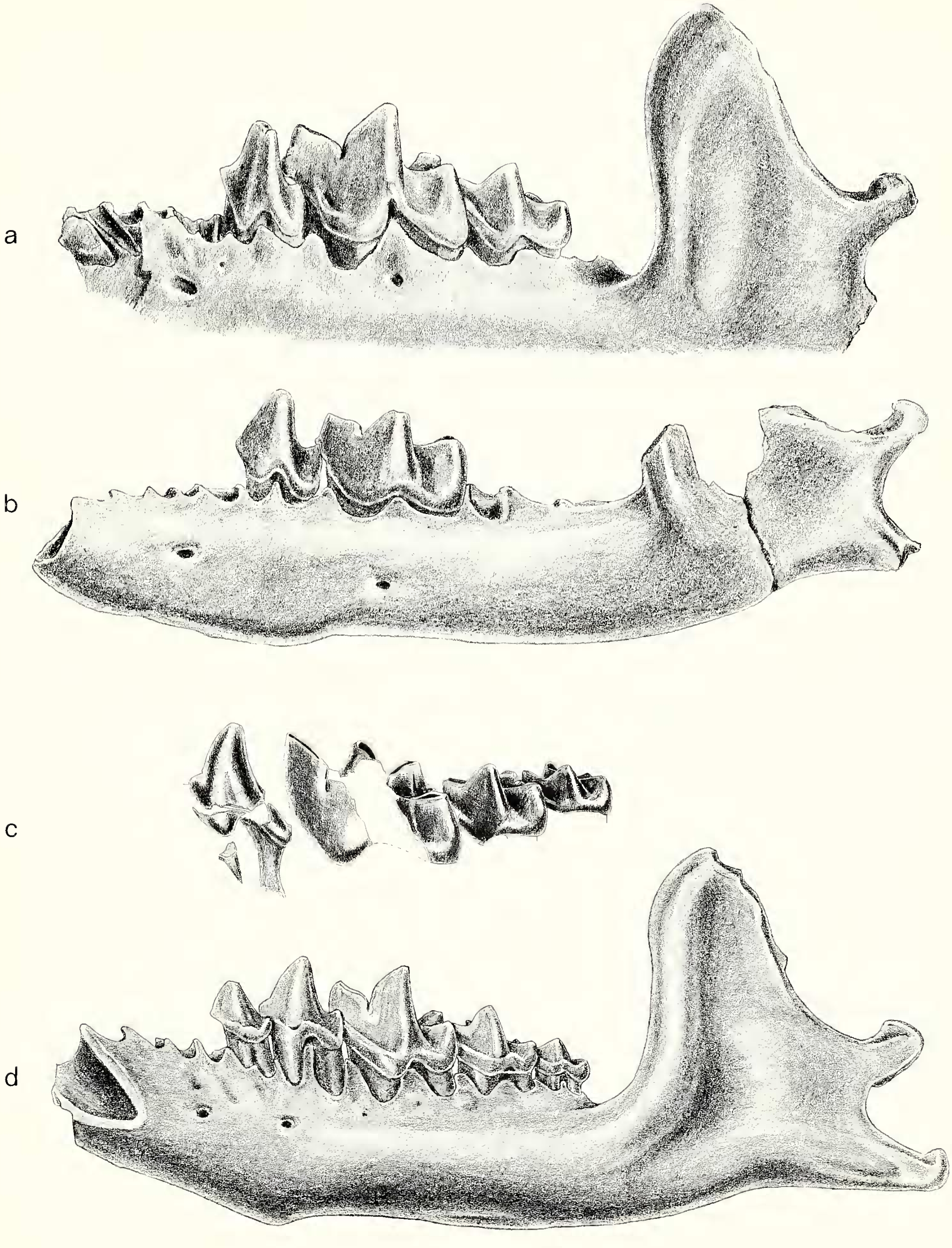

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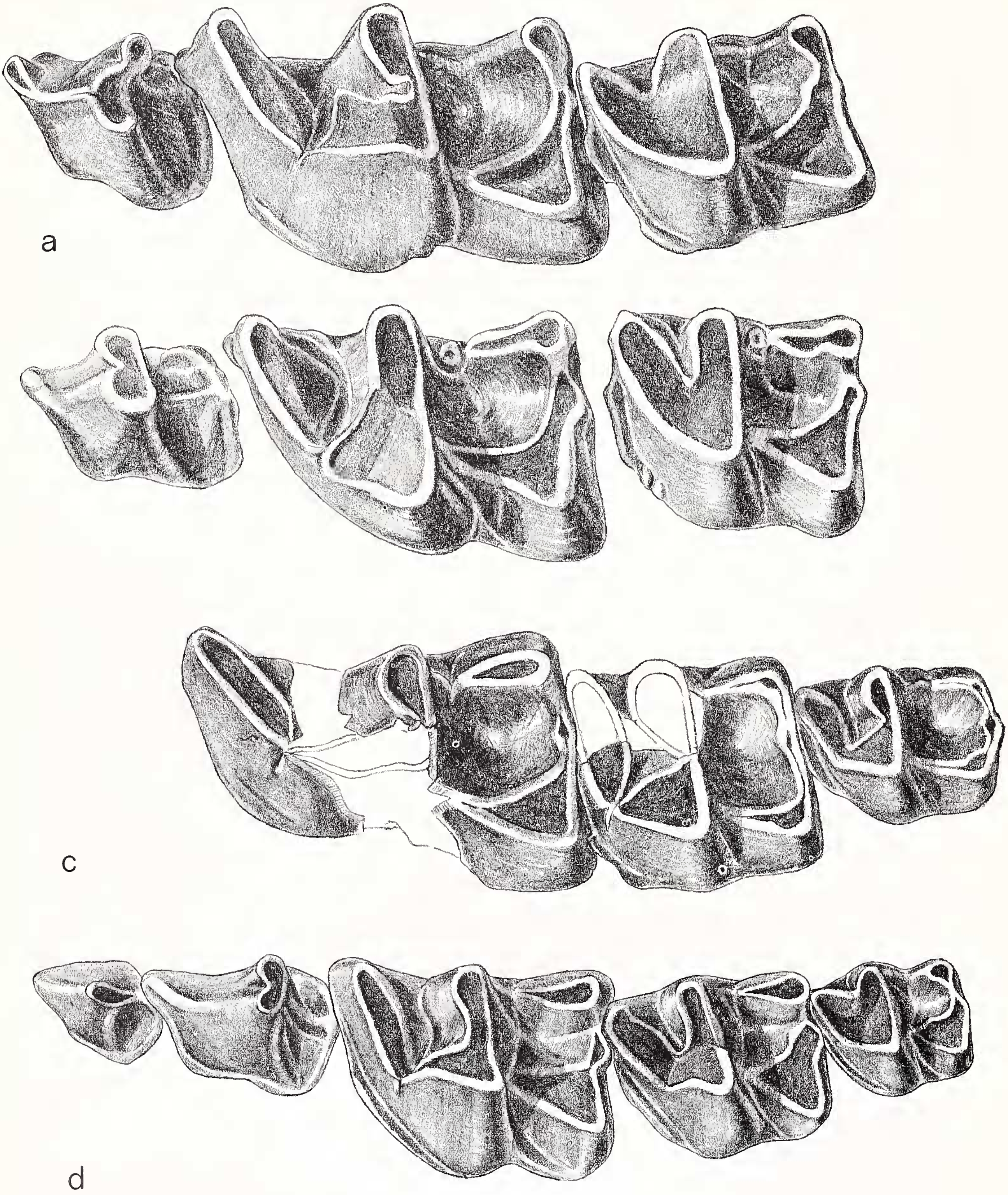

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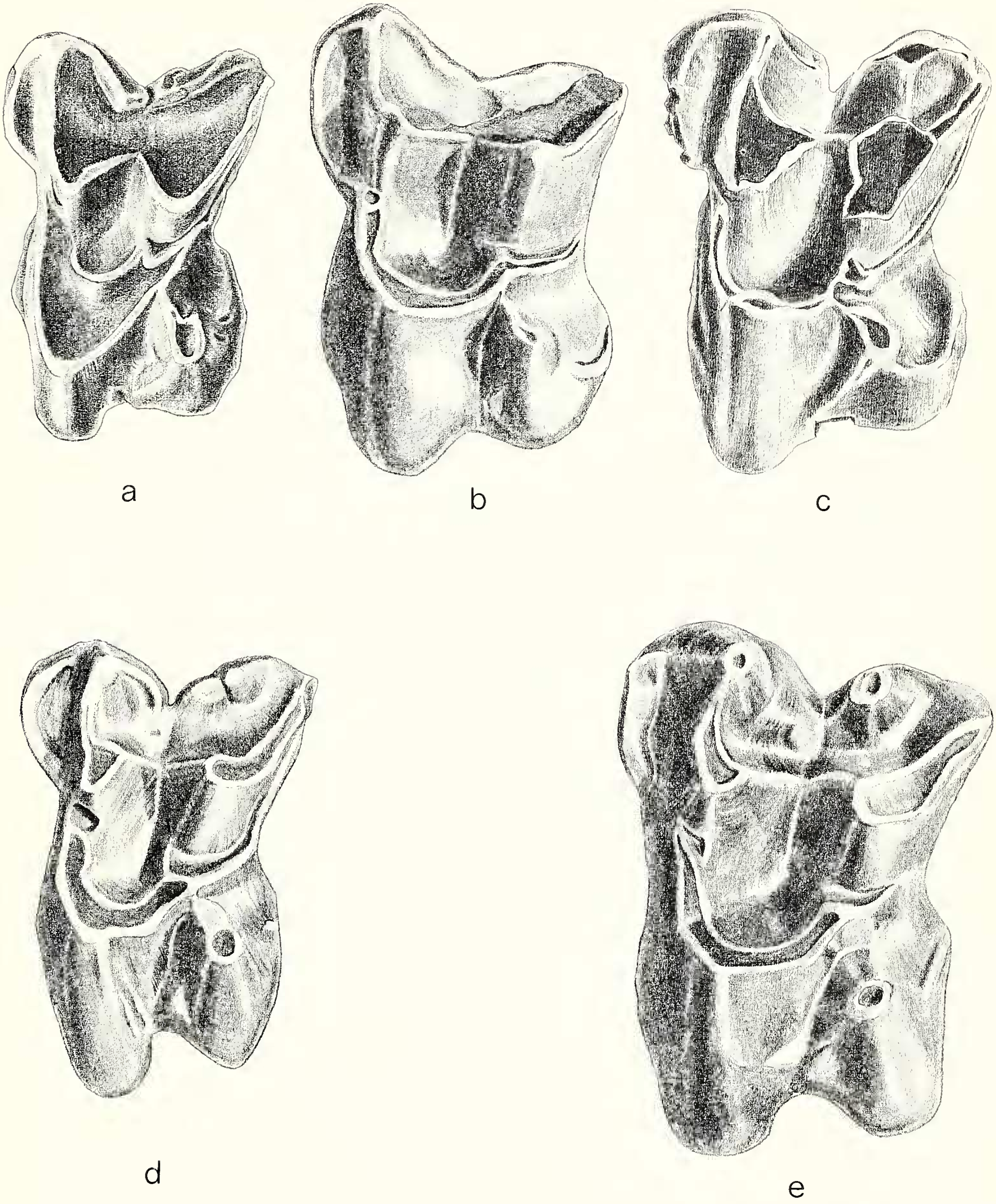

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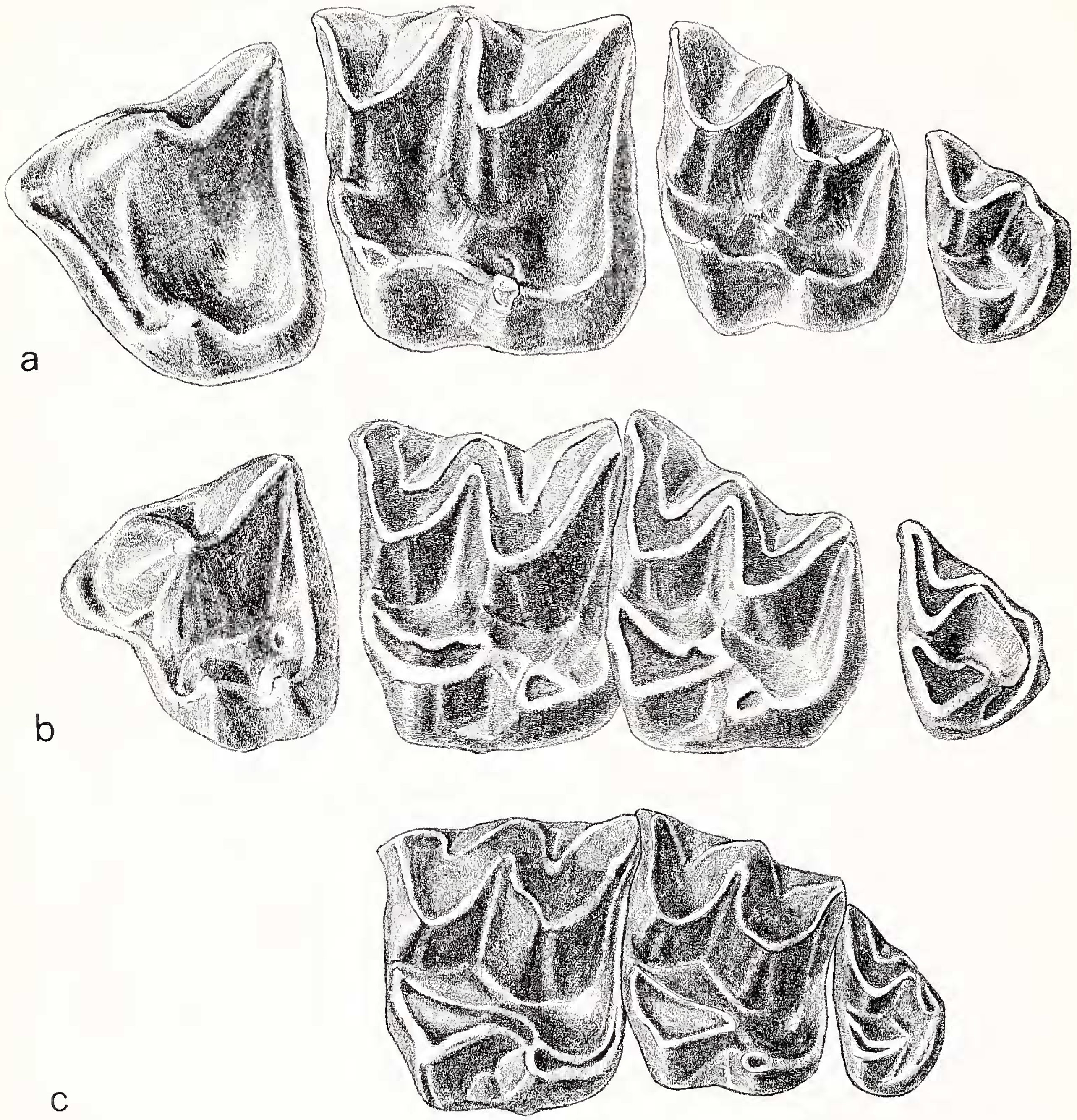

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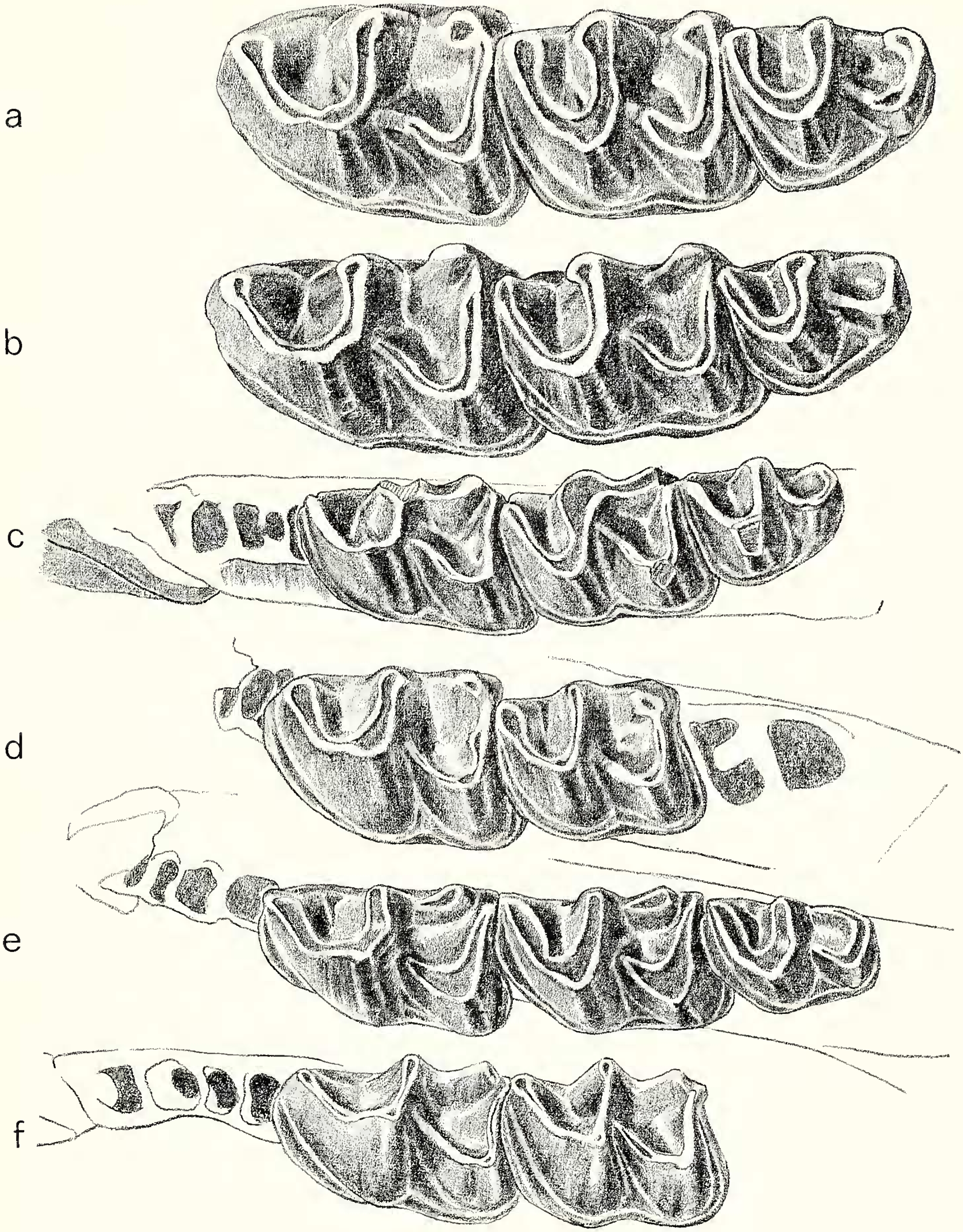

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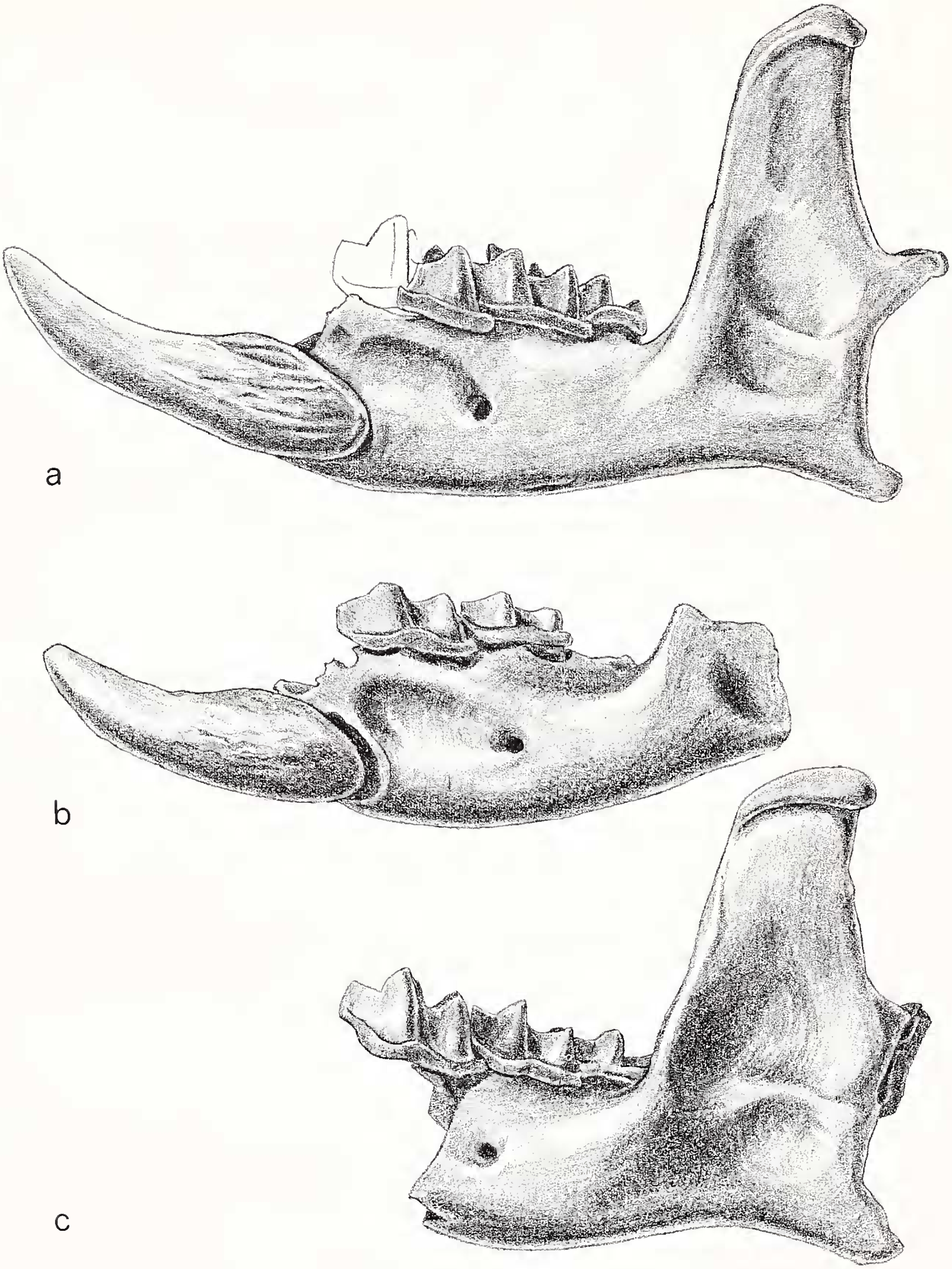

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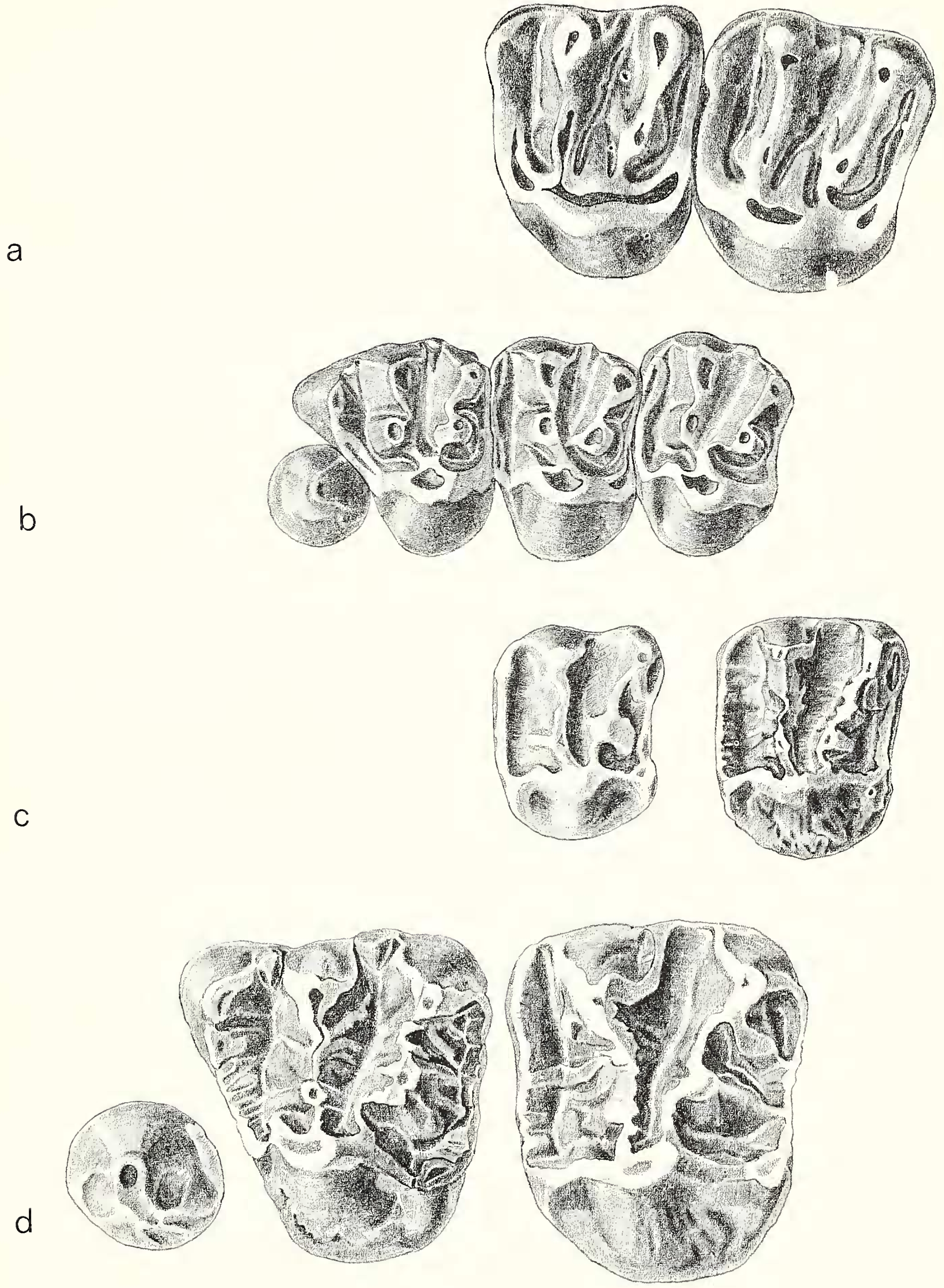

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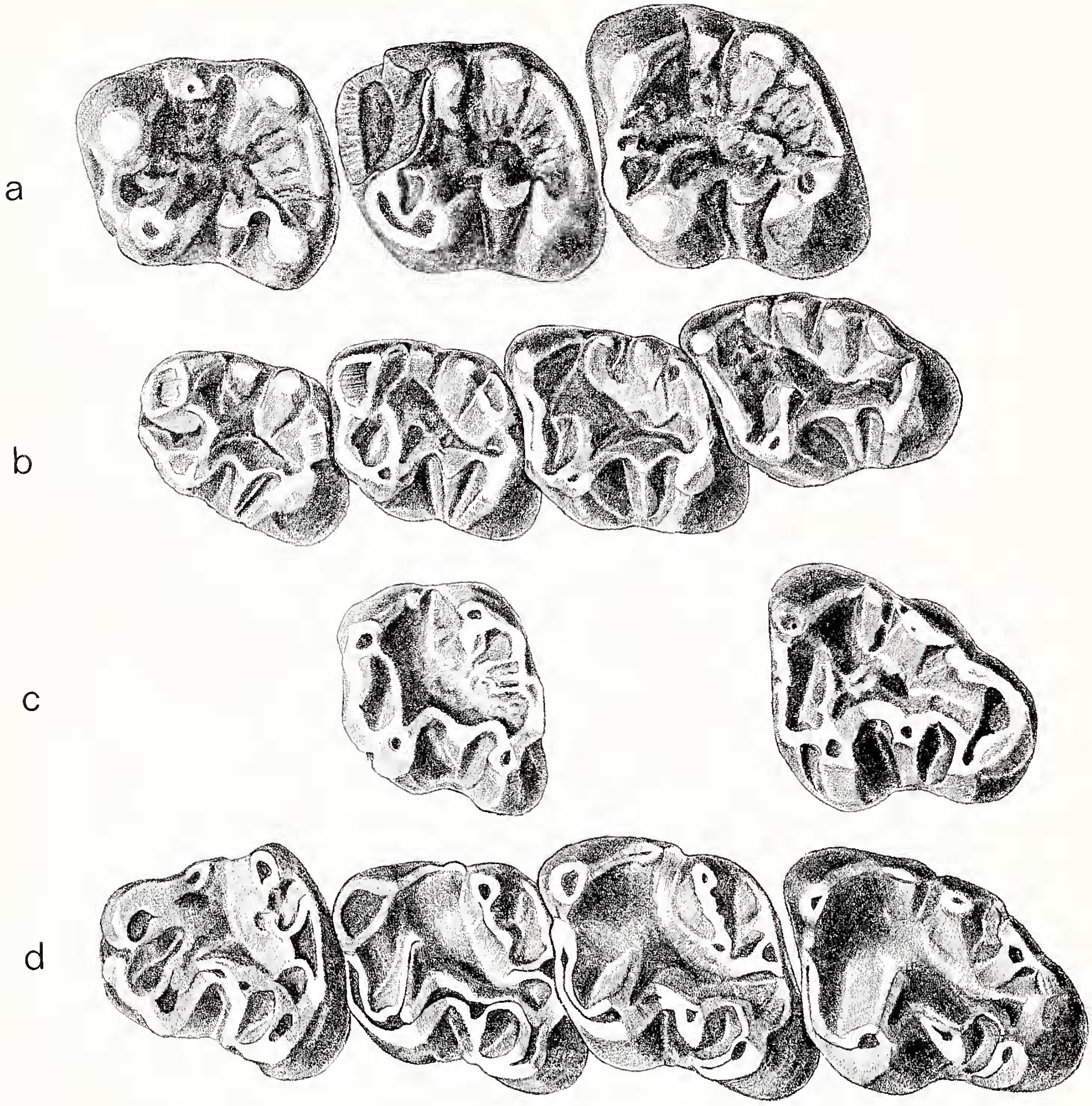

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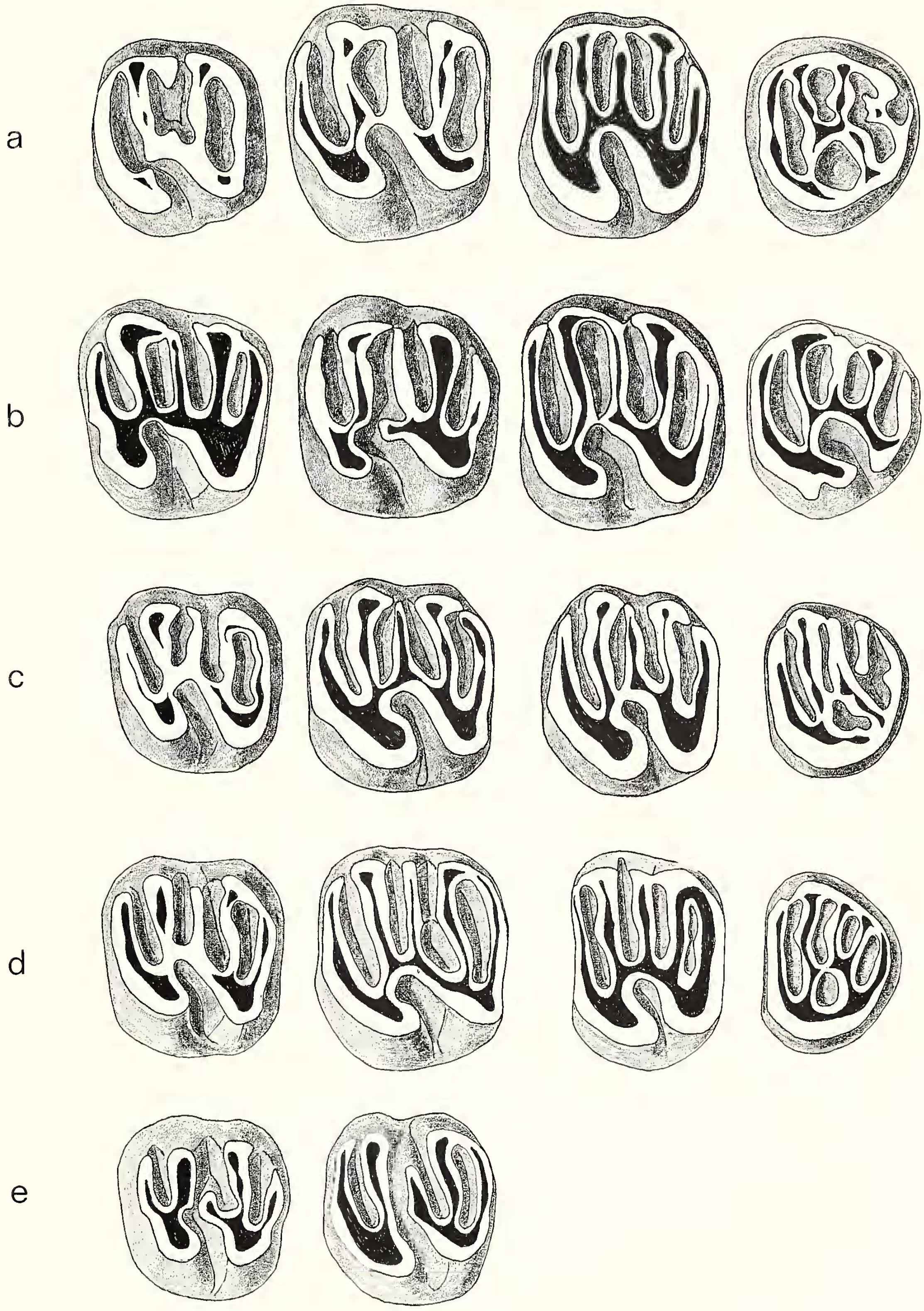

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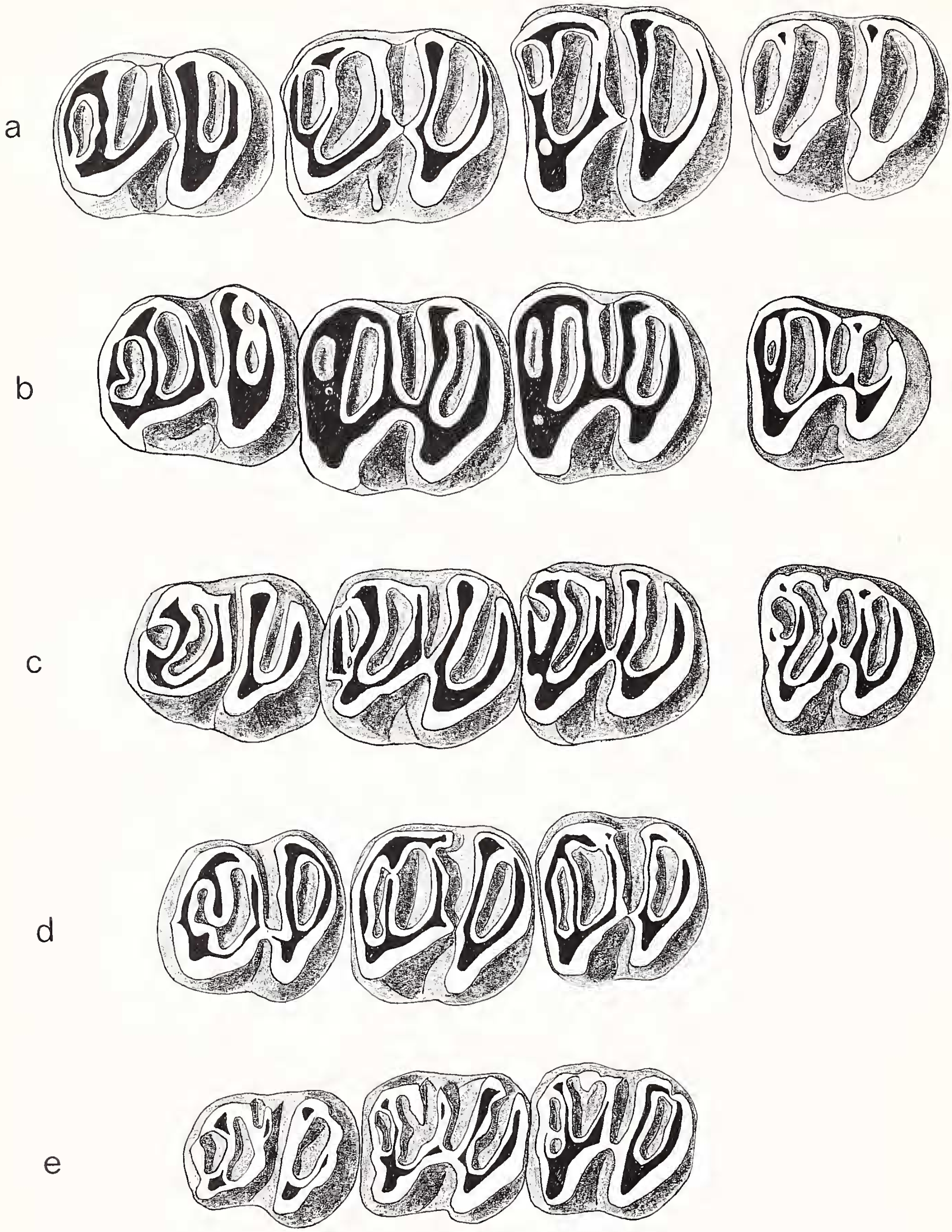

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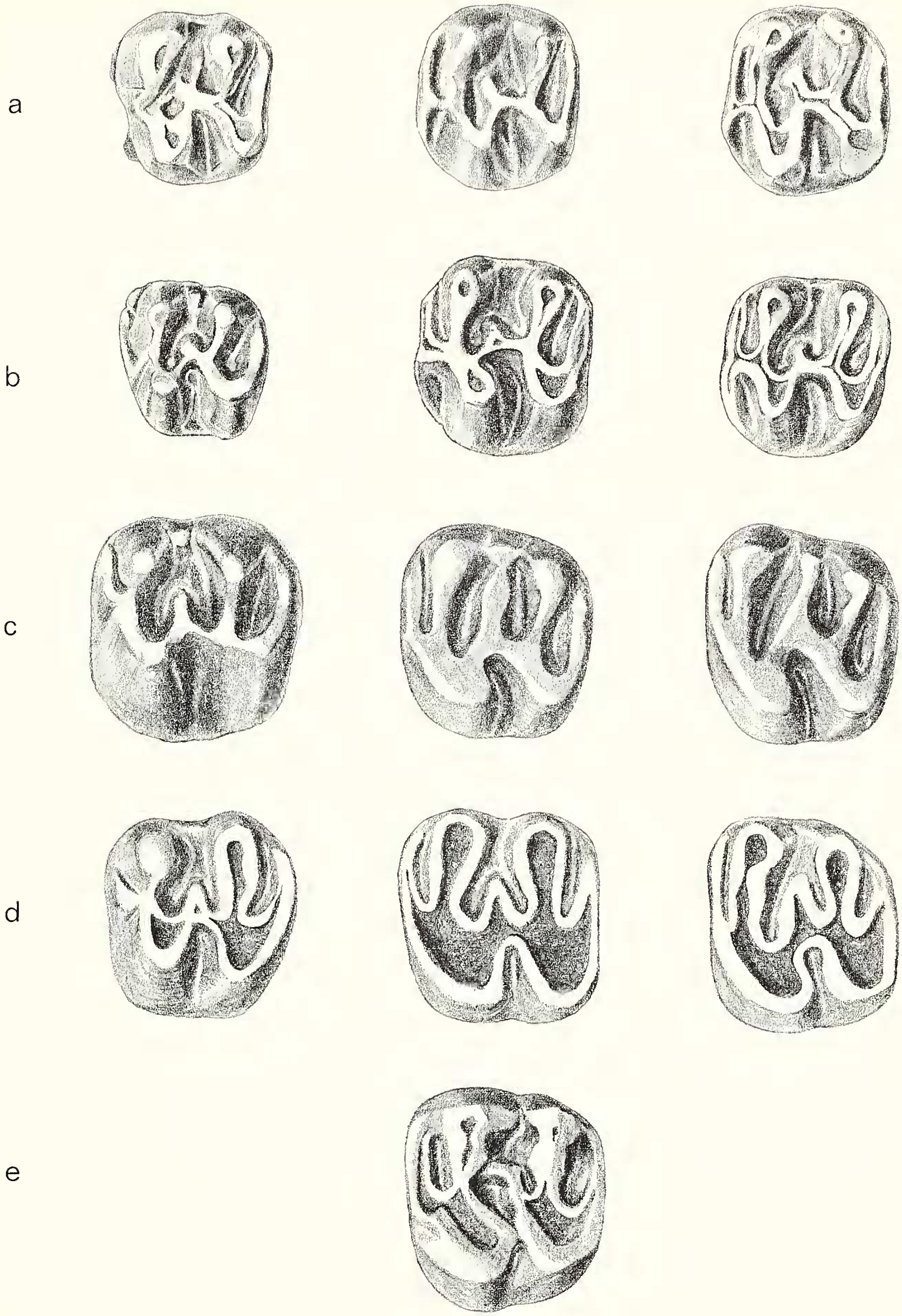

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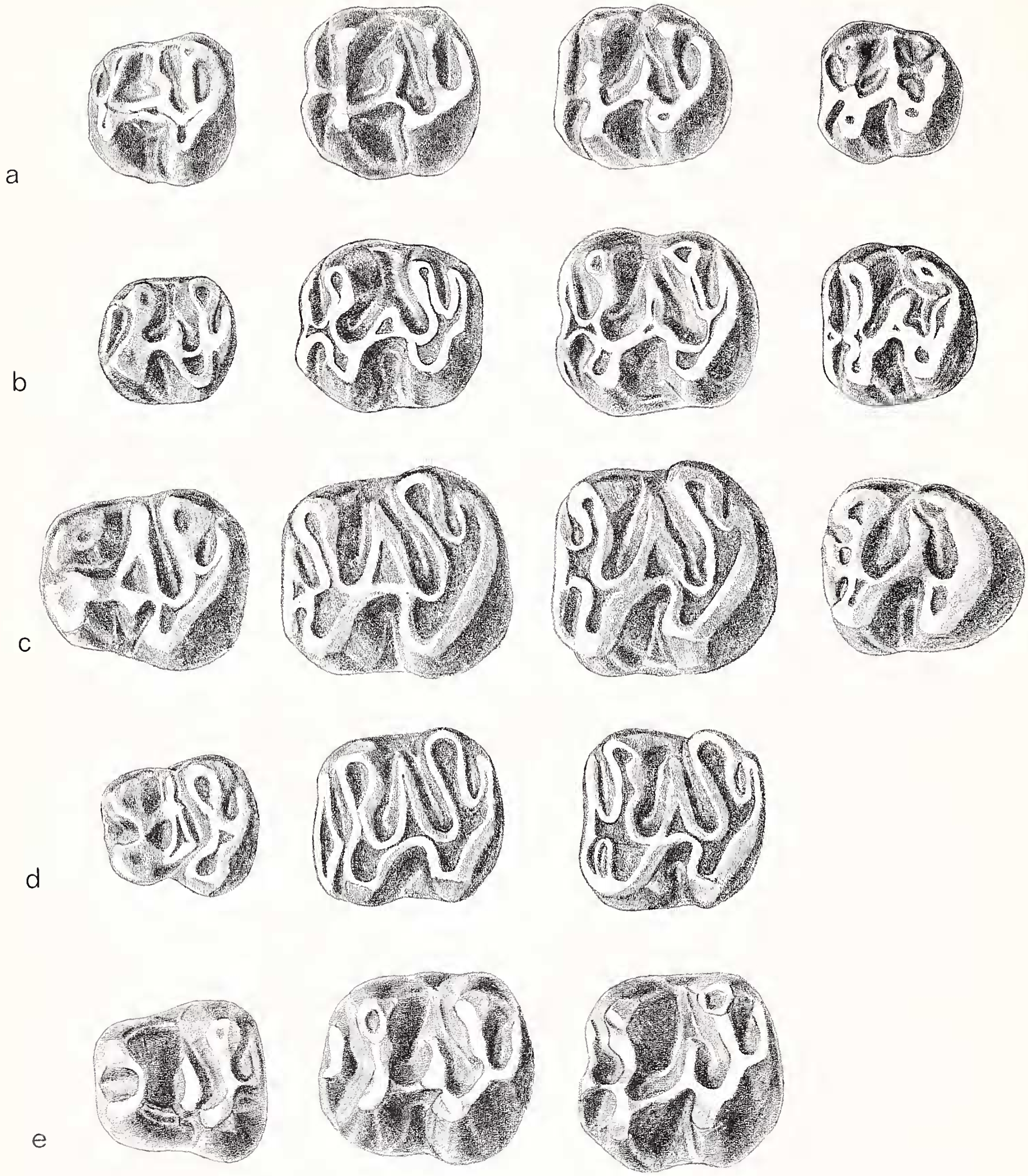

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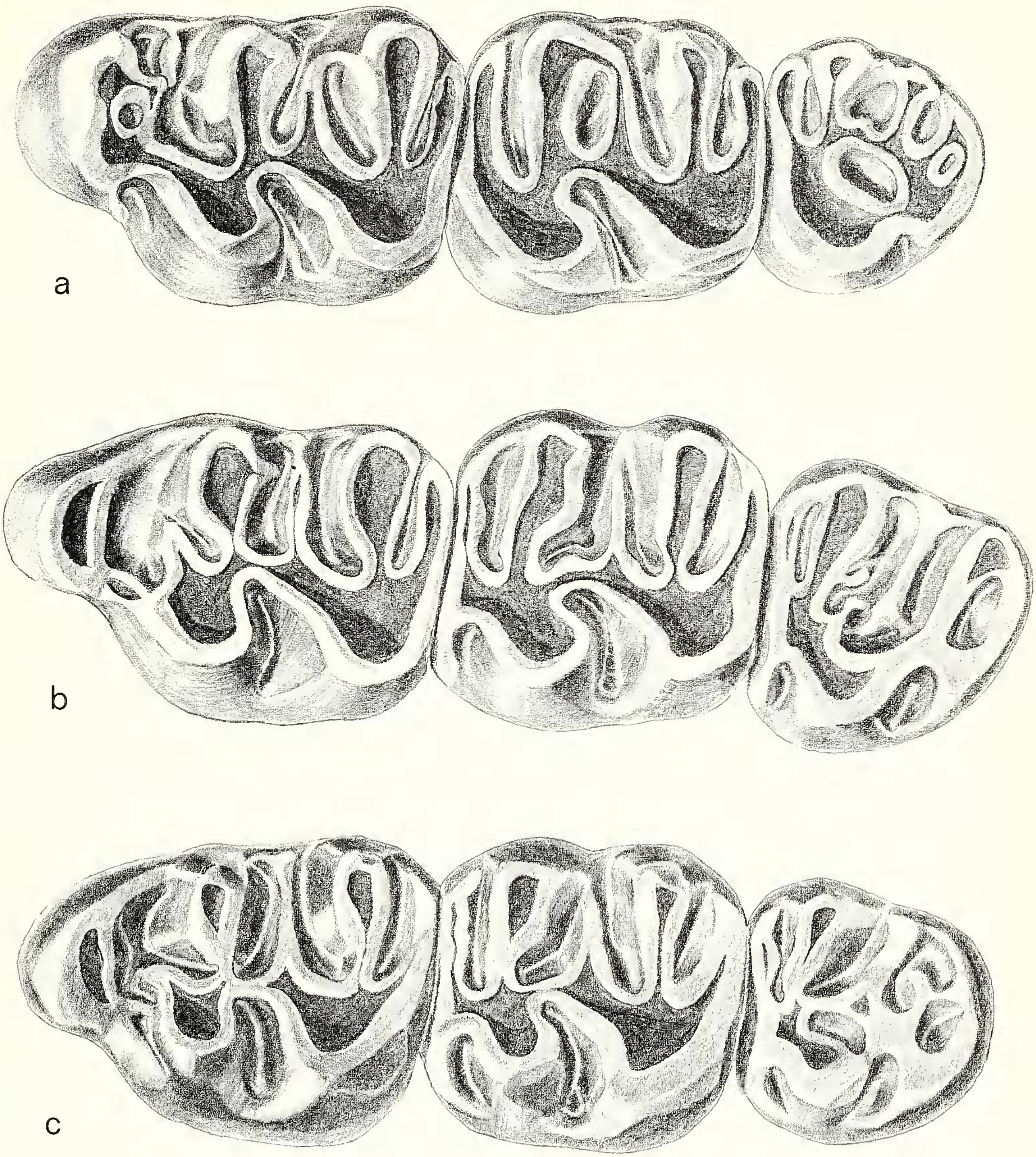

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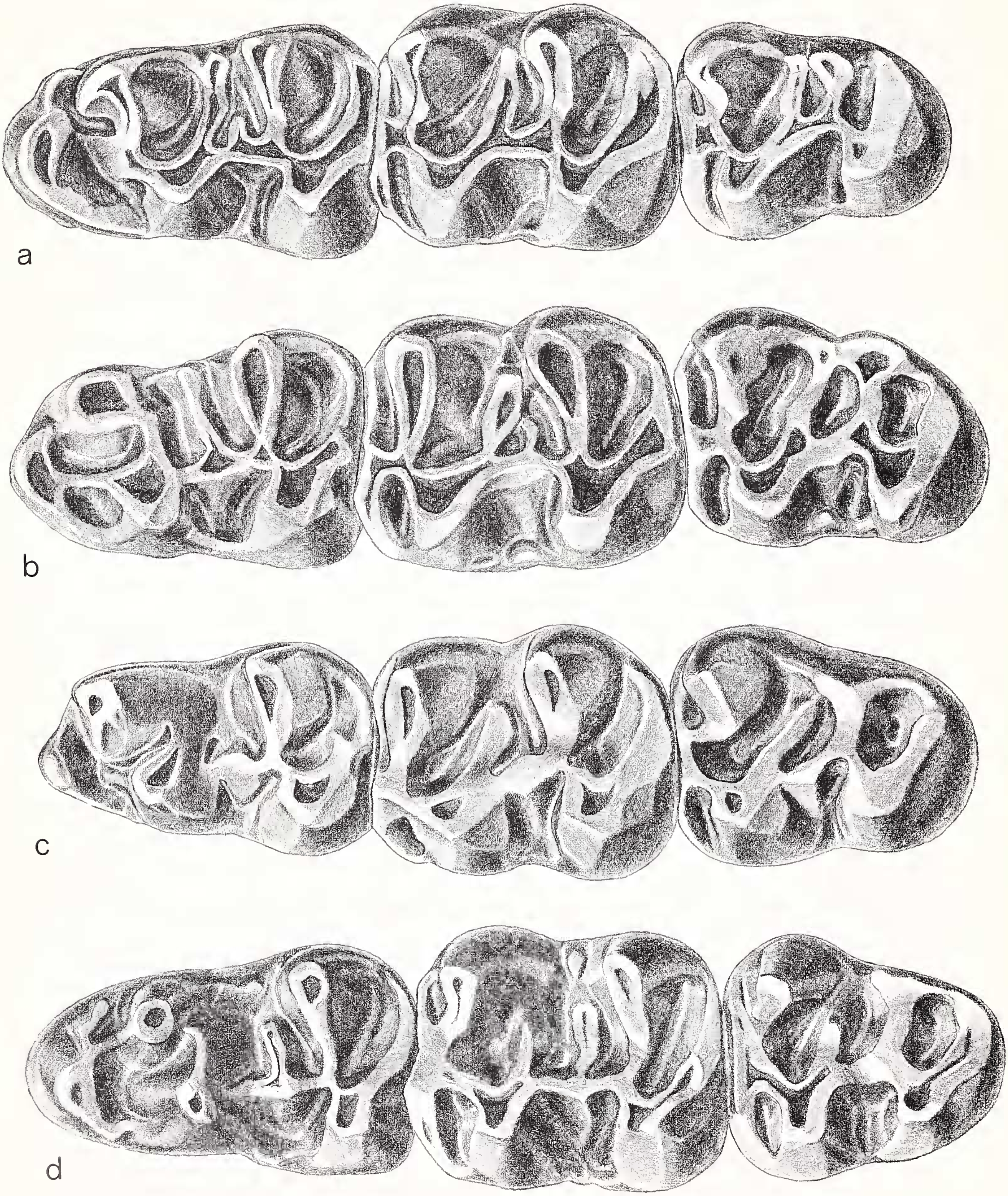

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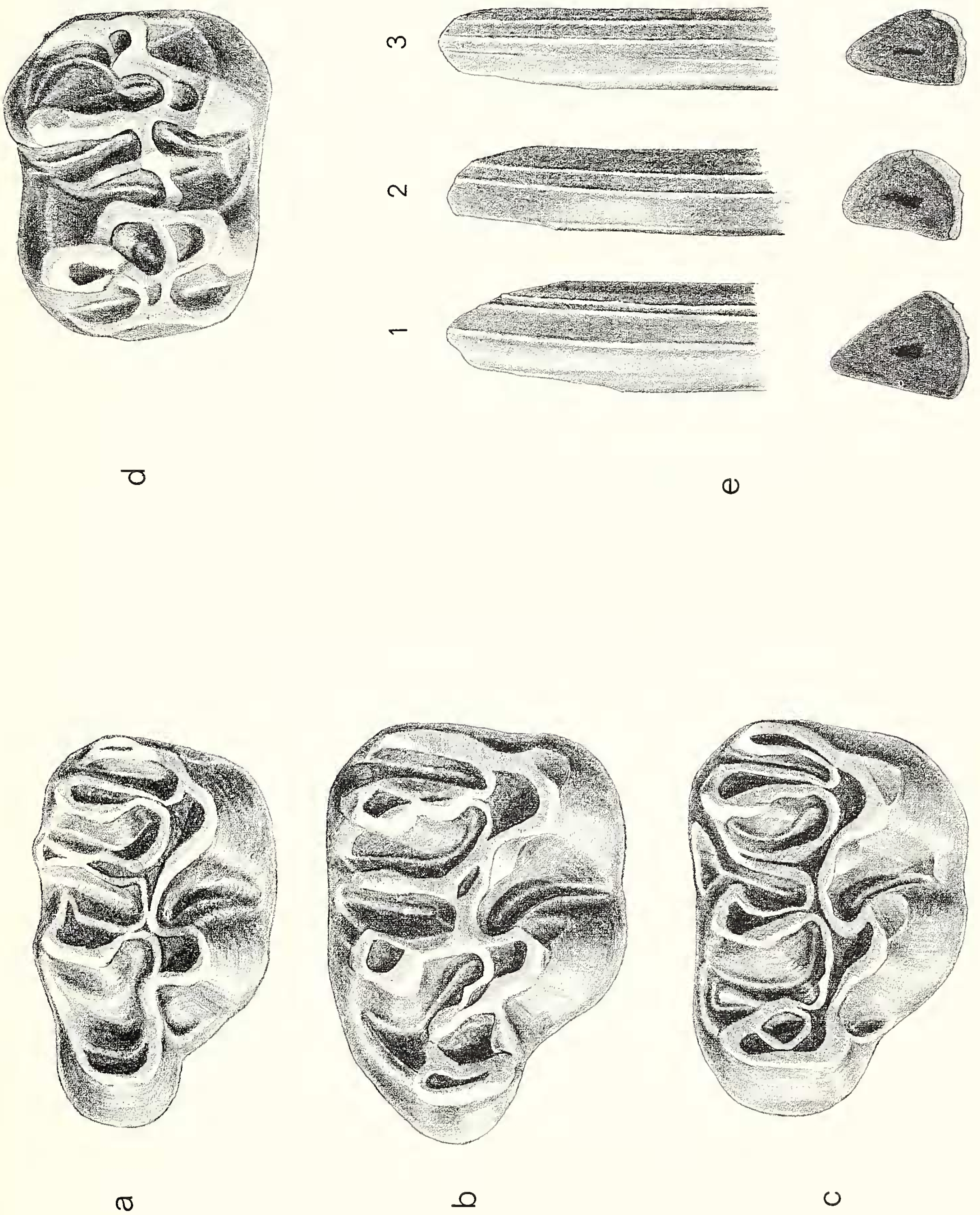

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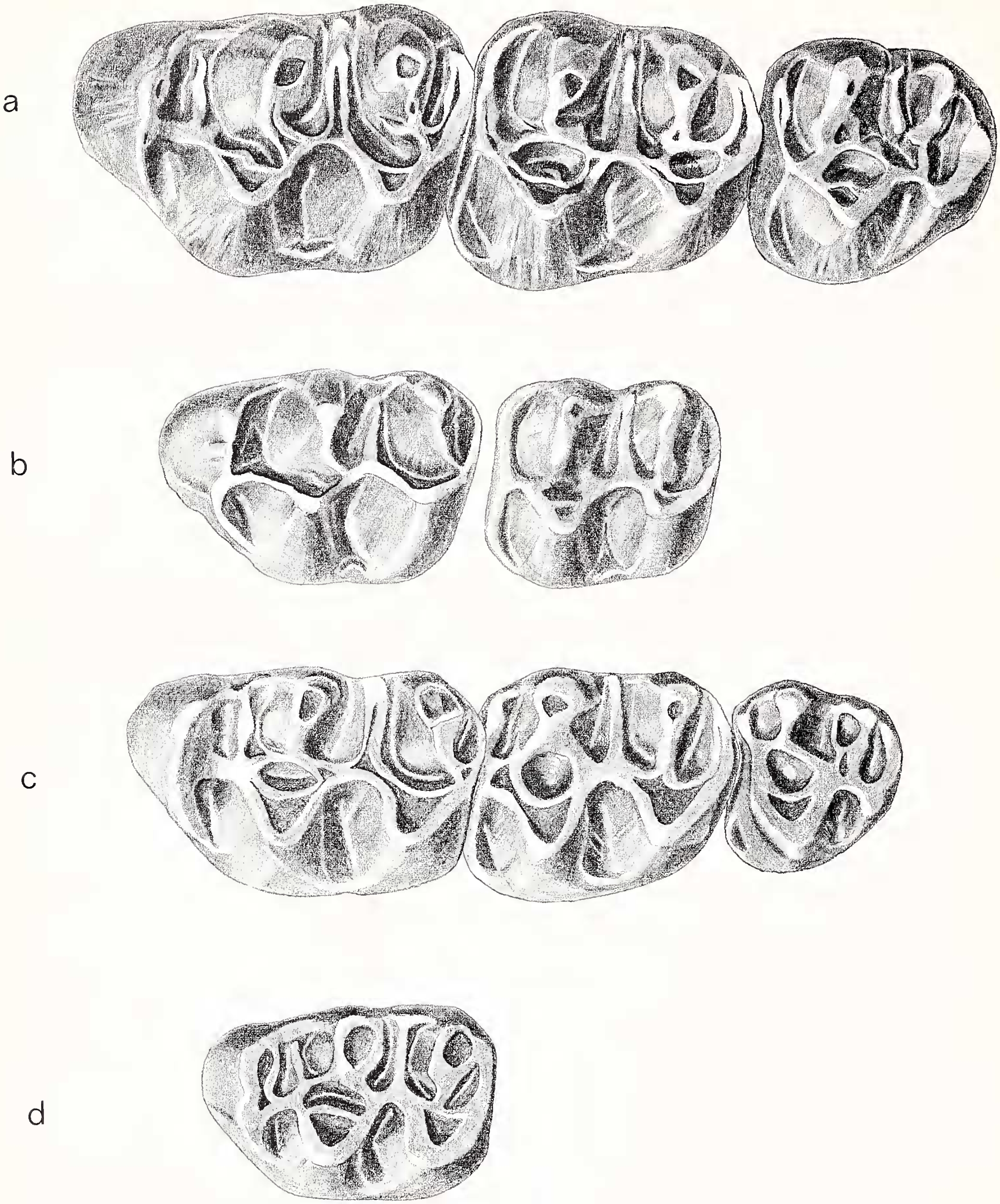

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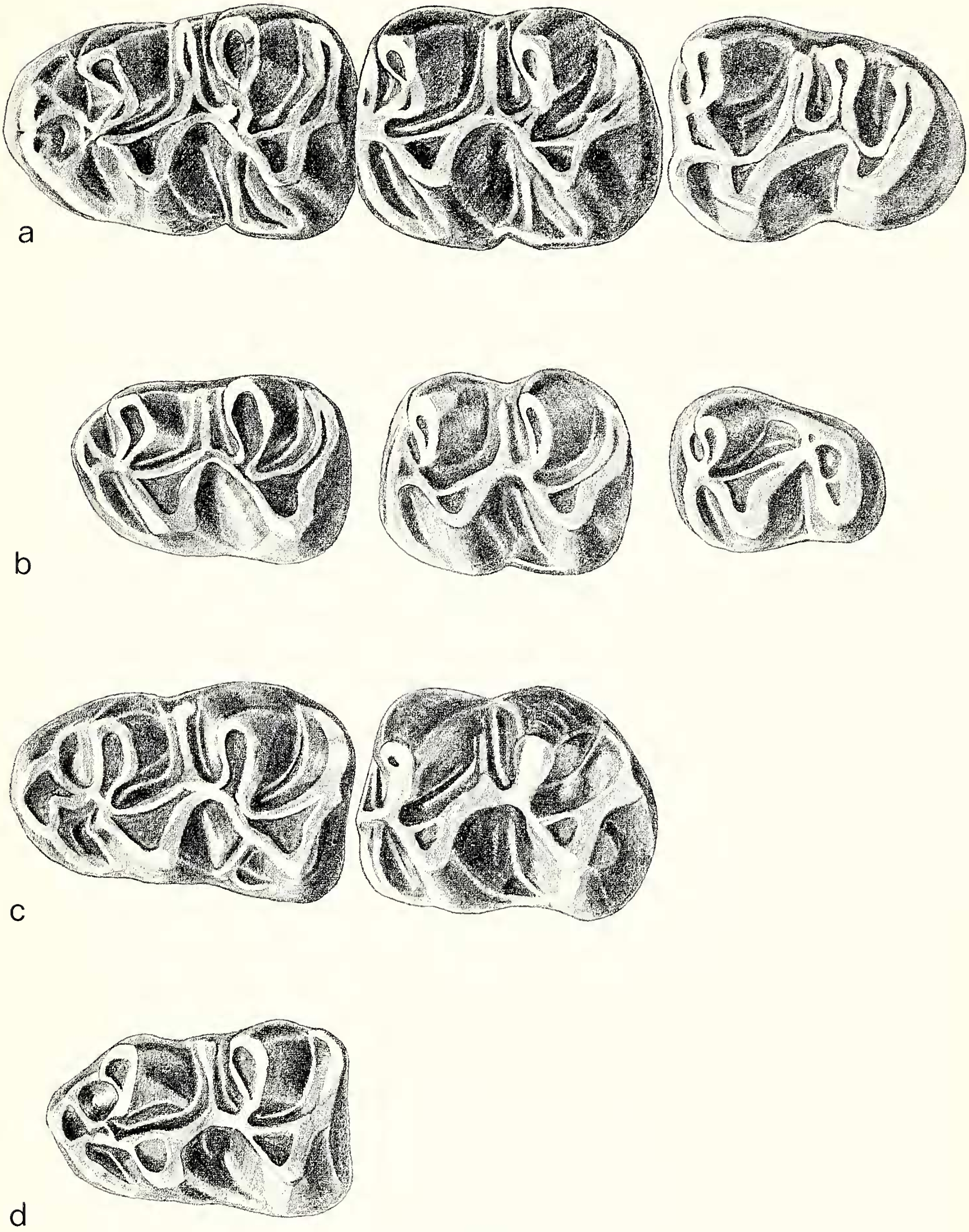

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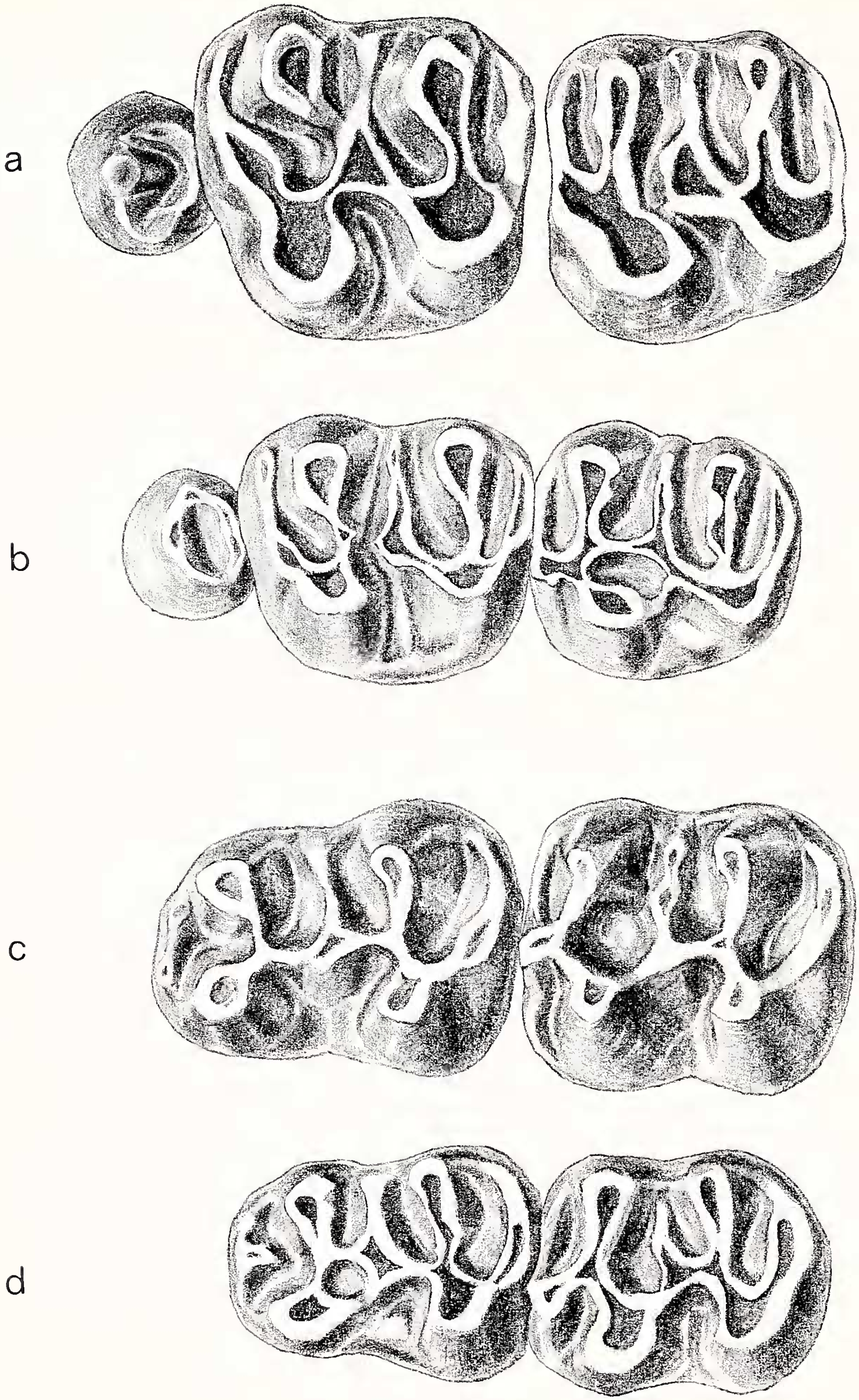

PLATE 20.